



Anisodactylus (Pseudaplocentrus) laetus Dejean. Lake Chicot State Park, Louisiana (body length of specimen 8.5 mm.).
Photograph by J. Scott.

THE ANISODACTYLINES (INSECTA:COLEOPTERA:CARABIDAE:
HARPALINI): CLASSIFICATION, EVOLUTION, AND ZOOGEOGRAPHY

GERALD R. NOONAN

Department of Entomology

The University of Alberta

Edmonton, Alberta T6G 2E3

Quaestiones entomologicae
9:266-480 1973

The North American species of *Anisotarsus Chaudoir*, *Notiobia* (s. str.) *Perty*, and *Gynandrotarsus LaFerté* together with all supra-specific taxa of the subtribe Anisodactylina are revised. Keys and descriptions are provided to revised species and all supra-specific taxa. Morphological characters useful in distinguishing taxa are discussed and illustrated. Synonyms of revised taxa are listed and reasons for regarding them as synonyms discussed. Where necessary, lectotypes, neotypes, and type species are designated. The distribution of each revised species is described in the text and also illustrated by a map. Geographical and intrapopulational variation of the revised species are analyzed, and available information on flight and bionomics is also presented.

The genus-group taxa *Notiobia* (s. str.) and *Anisotarsus* are treated as subgenera of *Notiobia* (s. lat.). Thirteen species are recognized in the subgenus *Anisotarsus*; one of these, *schlingeri* (type locality 12.4 mi. s. Tecalitlan, Jalisco, Mexico) is new. Ten species are recognized in the subgenus *Notiobia* with *cooperi* (type locality Tepic, Nayarit, Mexico) and *ewarti* (type locality Coyame, Lake Catemaco, Veracruz, Mexico) being new species. The subgenus *Gynandrotarsus* (genus *Anisodactylus*) is considered to have 10 valid species, including a new one, *darlingtoni* (type locality e. of Morelia on Rte. 15, Michoacan, Mexico).

Thirty-seven genera and subgenera and 24 genera are regarded as members of Anisodactylina. Three of the 37 genera and subgenera are new: the genus *Pseudanisotarsus* (type species *Anisotarsus nicki* van Emden, 1953); and the subgenera *Pseudanisodactylus* (type species *Anisodactylus punctatipennis* Morawitz, 1862) and *Pseudaplocentrus* (type species *Anisodactylus laetus* Dejean, 1829) of the genus *Anisodactylus*. The subgeneric name "Pseudohexatrichus" (genus *Anisodactylus*) is validated with *Anisodactylus dejani* Buquet, 1840 designated as type species. *Progonochaetus basilewskyi* is proposed as a replacement name for *Dichaetochilus jeanneli* Basilewsky, 1946 because both *D. jeanneli* Basilewsky, 1946 and *Rasnodactylus jeanneli* Basilewsky, 1946 are regarded as members of the genus *Progonochaetus*.

The phylogenies of the supra-specific taxa and revised species of *Anisotarsus* and *Gynandrotarsus* are reconstructed by cladistic techniques slightly modified from those proposed by Hennig. Analysis of the supra-specific reconstructed phylogeny indicates: that primitive taxa are concentrated in the Australian Region with more derived ones concentrated in the Northern Hemisphere; and that now widely separated continents such as Africa and South America contain "sister" taxa (sensu Hennig). It is postulated that the Anisodactylines evolved on the combined continents of Australia and Antarctica during late Jurassic or early Cretaceous and dispersed northward during phases of continental drift. The zoogeography of the genera and subgenera of Anisodactylina is discussed in detail.

Study of the reconstructed phylogeny of North American species of *Anisotarsus* and examination of South American species suggest that the North American species are derived from 2 separate invasions of South American ancestors. Present North American species distributions are studied and explained by reference to past North American climatic, geological, faunal, and floral changes.

Since the closest cladistic relatives of many North American species of *Notiobia* (s. str.)

seem to be Middle or South American forms which are poorly known, it is concluded that reconstruction of the phylogeny of North American species must be deferred.

The closest cladistic relative of *Gynandrotarsus* is *Pseudodichirus* which is the more primitive of the 2 groups and is found in Europe. It is postulated that the ancestor of *Gynandrotarsus* crossed from Europe to North America during very late Cretaceous or early Tertiary via the then broad land connection between Europe and eastern North America. Present species distributions are studied and explained by reference to past North American climatic, geological, faunal and floral changes.

Les espèces nord-américaines d'Anisotarsus Chaudoir, Notiobia (s. str.) Perty et Gynandrotarsus LaFerté et tous les taxa supragénériques de la sous-tribu Anisodactylina sont revus. Des clefs et des descriptions sont pourvues pour les espèces revues et pour tout taxa supra-spécifiques. Tout caractère morphologique jugé utile est discuté et illustré. Une liste des synonymes est pourvue, et chaque cas est discuté. Lorsque nécessaire, les lectotypes, les néotypes et les espèces type sont désignés. La distribution géographique de chaque espèce revue est décrite dans le texte et illustré par une carte géographique. Les variations géographiques et les variations à l'intérieur des populations est analysées pour les espèces revues, et lorsque l'information est disponible les données sur le vol et la bionomique sont présentées.

Les genres Notiobia (s. str.) et Anisotarsus sont traités comme sous-genres des Notiobia (s. lat.). Treize espèces sont reconnues dans le sous-genre Anisotarsus; l'une d'elle est nouvelle, schlingeri (localité type 12.4 mi. s. Tecalitlan, Jalisco, Mexico). Dix espèces sont reconnues dans le sous-genre Notiobia avec cooperi (localité type Tepic, Nayarit, Mexico) et ewarti (localité type Coyame, lake Catemaco, Veracruz, Mexico) comme espèces nouvelles.

*Trente-sept genres et sous-genres, et 24 genres sont reconnus comme membres des Anisodactylina. Trois d'entre eux sont nouveaux: le genre *Pseudanisotarsus* (espèce type Anisotarsus nicki van Emden, 1953); et dans le genre *Anisodactylus* les sous-genres *Pseudanisodactylus* (Espèce type *Anisodactylus punctatipennis* Morawitz, 1862) et *Pseudaplocentrus* (espèce type *Anisodactylus laetus* Dejean, 1829). Le nom sous-générique "Pseudhexatrichus" du genre *Anisodactylus* est valide, et l'*Anisodactylus dejeani* Buquet, 1840 est désigné comme l'espèce type. *Progonochaetus basilewskyi* est proposé comme un nom de remplacement pour *Dichaetochilus jeanneli* Basilewsky, 1946 car *D. jeanneli* Basilewsky, 1946, et *Rasnodactylus jeanneli* Basilewsky, 1946 sont considérés comme membres du genre *Progonochaetus*.*

Les phylogénies des taxa supra-spécifiques et des espèces d'Anisotarsus et de Gynandrotarsus sont reconstruites au moyen de techniques cladistiques légèrement modifiées de celles proposées par Hennig. L'analyse de la phylogénie reconstruite pour les taxa supra-spécifiques indique que les taxa primitifs sont concentrés dans la région Australienne, que les plus évolués sont concentrés dans l'hémisphère nord, et que l'Afrique et l'Amérique du sud, malgré les grandes distances entre elles, contiennent présentement des taxa soeurs. Il est postulé que les Anisodactylines ont évolué sur les continents combinés d'Australie et d'Antarctique à la fin du Jurassique ou au début du Crétacé, et plus tard ils se dispersèrent vers le nord durant les phases de la dérive continentale. La zoogéographie des genres et sous-genres des Anisodactylina est discutée en détail.

L'étude de la phylogénie reconstruite des espèces d'Anisotarsus nord américains et l'examen des espèces sud américaines suggèrent que les espèces nord américaines sont originées lors de deux invasions d'ancêtres sud américains. La distribution présente des espèces nord américaines sont étudiée et expliquée en relation aux anciens climats, et changements géologiques, faunistiques et floristiques en Amérique du nord.

Comme les espèces les plus voisines cladistiquement de plusieurs espèces nord américaines de *Notiobia* (s. str.) semblent appartenir à des formes peu connues l'Amériques central et d'Amérique du sud, il est conclu que la reconstitution de la phylogénie des espèces nord américaines doit être remise à plus tard.

Le sous-genre le plus voisin cladistiquement des *Gynandrotarsus* est *Pseudodichirus* qui est le moins évolué des deux groupes. Ce dernier sous-genre est trouvé en Europe. Il est postulé que l'ancêtre des *Gynandrotarsus* traversa d'Europe à l'Amérique du nord à la fin du Crétacé ou au début du Tertiaire par une connection terrestre très large entre l'Europe et l'est de l'Amérique du nord. La distribution présente des espèces est étudiée et expliquée en relation aux anciens climats, et aux changements géologiques faunistiques et floristiques nord américains.

CONTENTS

Introduction	269
Materials	269
Methods	270
Systematics	276
Phylogeny	382
Zoogeography	403
Acknowledgements	417
Literature Cited	418
Tables	428
Figures	447

INTRODUCTION

My interest in the subtribe Anisodactylina began in 1967 when I revised the species of the genus *Dicheirus*, a member of Anisodactylina. In order to better understand the relationships of *Dicheirus* to other genera of Carabidae, I examined specimens of other groups of Anisodactylina and reviewed the literature on the subtribe. I found that the supra-specific classification of the subtribe was in great need of revision since workers had added and deleted genera until one could only state that the subtribe contained approximately 40 genera. I also found that the species of many genera and subgenera of Anisodactylina were in need of revision.

I have undertaken a comprehensive 5 part study of the Anisodactylina: (1) a reclassification of the supra-specific taxa of the subtribe on a world-wide basis; (2) revisions of the species of *Gynandrotarsus* and the North American species of *Notiobia*; (3) a revision of the species of the subgenus *Anadaptus*; (4) a revision of the Central and South American species of *Notiobia*; and (5) revisions of the species of the Australian and Oriental genera. The first and second parts are now presented. My revisions of *Gynandrotarsus* and North American *Notiobia* (including *Anisotarsus*) used with Lindroth's (1968) excellent treatment of the Harpalini of Canada and Alaska treat all North American species of Anisodactylina except a few species of the subgenus *Anadaptus*.

MATERIALS

The taxonomic decisions in this paper are based on a comparison of characters found in adult specimens. Approximately 15,000 adult specimens were examined for the supra-

specific reclassification. An additional 10,533 specimens were examined for the revisions of the species of *Gynandrotarsus* and the North American species of *Notiobia*.

Types were examined during visits to the British Museum of Natural History, London, Great Britain; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; Museum National d'Histoire Naturelle, Paris, France; and United States National Museum, Washington, D.C. Unless otherwise noted, I have seen the type of each species (and associated synonyms) of *Gynandrotarsus* and of the North American forms of *Notiobia*. In addition I have seen type or identified specimens of most of the species in other supra-specific taxa of Anisodactylina. The museums from which non type material was examined are listed in the acknowledgements section.

METHODS

Criteria for species, subunits of species and supra-specific taxa

For this study the following definition of a species given by Mayr (1969) is accepted: a species consists of "Groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups". There is no direct information available on the presence or absence of interbreeding among forms in *Gynandrotarsus* and *Notiobia*. Also there is at most limited information on the ecology and biology of the various forms. Therefore the presence or absence of interbreeding must be inferred from an examination of color and of morphological characters. The underlying assumption of such an inference is that different species will be separated by a pronounced gap in color and/or morphological characters. I use the following criteria in delimiting species. Sympatric forms were considered to be separate species if they constantly differed in 1 or more color or morphological characters. Allopatric forms were considered as separate species if they differed in 1 or more color or morphological characters, and if the differences in these character(s) were roughly comparable to those found between other closely related species which were sympatric. None of the forms examined in this study exhibited parapatry.

Subspecies are not formally named in this paper. Characters other than those of morphology and color should be available for the recognition of formal taxa below the species level. Also a formal subspecific name has legal nomenclatural status and once proposed can never be abolished. I have therefore chosen to refer to subunits of species as "morphs". This is an informal term and names given to morphs need not be retained by subsequent workers who may disagree with my findings.

Simpson (1961) and Whitehead (1972) pointed out that the inclusiveness of genus group taxa is somewhat arbitrary. Hennig (1966) and Brundin (1966) asserted that supra-specific taxa which demonstrate sister group relationships must be given equal formal rank. This requirement is overly simplistic, leads to excessive splitting, and requires the recognition of numerous supra-specific categories in addition to the formally established ones such as subgenus, genus, subtribe, and tribe. Ball and Erwin (1969), Erwin (1970), and Darlington (1970) have objected to this requirement. Mayr (1969) listed 5 criteria for delimiting and ranking supra-specific taxa: (1) distinctness (size of gap); (2) evolutionary role (uniqueness of adaptive zone); (3) degree of difference (that is evolutionary divergence); (4) size of taxon; and (5) equivalence of ranking in related taxa. I have endeavored to take account of these 5 criteria in delimiting and ranking supra-specific taxa.

I have for the most part recognized only monophyletic supra-specific taxa, that is taxa composed of all the descendants of an immediate common ancestor. However, consideration of the criteria provided by Mayr has led me to recognize several paraphyletic groups. For example, the genus *Geopinus* which most likely evolved from the same common ances-

tor as several subgenera of the genus *Anisodactylus* is accorded separate generic status because of the large amount of evolutionary divergence and because of the ecological specialization of the single included species.

Procedural methods

Sorting of specimens employed in revisions of species.

Sorting of specimens was done according to a systematic procedure to facilitate application of the criteria explained above for species and "morphs". Specimens were first grouped into series each composed of specimens with similar color and external morphology. The specimens of each series were next sorted according to geographical locality. The specimens of a series were then compared in regard to color and external morphology. If this comparison indicated the members of a series were probably conspecific, then the genitalia were examined from specimens distributed throughout the entire range of the "tentative" species. If such an examination supported the hypothesis of conspecificity, then the series was compared with other such series to determine if any of these series were conspecific. Specimens of an individual series, which on an examination of the genitalia seemed to be composed of smaller subunits, were sorted into these subunits. The subunits were then carefully compared to determine whether they warranted separate specific status. Any subunits which seemed to warrant separate specific status were compared with all other "tentative" species.

After a species was delimited, all specimens of it were further examined for intra- and interpopulational variation. For this examination, it was assumed that specimens of a species collected at the same exact locality were members of a single deme.

Sorting of specimens employed in revisions of supra-specific groups.

Specimens were first sorted according to named species of currently accepted supra-specific taxa. The species of each such supra-specific taxon were then examined to determine if they formed a single monophyletic group. Adjustments were made if the species of a given taxon appeared to represent 2 or more monophyletic groups, to represent only part of a single monophyletic group, or to represent elements of several different monophyletic groups.

During the grouping process, a tentative phylogeny was constructed and repeatedly modified until it seemed the most probable representation of the evolution of supra-specific taxa of Anisodactylina. The units of species or species groups were finally ranked into genera, subgenera and species groups on the basis of the criteria explained above.

Dissecting techniques

Specimens in which the genitalia, hindwings, or mouthparts were to be removed were relaxed in boiling or nearly boiling distilled water for 2 to 5 minutes. Detergent such as "409 Household Cleaner" was usually added in order to simultaneously clean the beetle of any dust or grease. The specimen was next placed for 1 to 2 minutes in a beaker of distilled water to wash away any detergent residue. Watchmaker forceps with number 5 points were used for the dissections described below.

The genitalia could usually be removed through the genital opening. Forceps were inserted into the opening and moved from side to side to enlarge it. The genitalia were then grasped near their base and pulled out. This extraction procedure did not work on specimens which had been killed or preserved in formalin or alcohol solutions. In these specimens the abdomen was pulled off and the genitalia removed after cutting or tearing away the tergum.

The internal sac of the median lobe was then everted on several male specimens. The median lobe was first placed in boiling or nearly boiling 5 to 10 percent potassium hydroxide solution for 3 to 5 minutes to dissolve muscle tissue attached to the internal sac. Then

the median lobe was transferred to a small water-filled watch glass or a plastic lid from a prescription vial. A pair of forceps was used to clamp the basal bulb dorso-ventrally just distal to the basal orifice. These forceps were kept clamped in order to prevent fluid from escaping through this opening. A second pair of forceps was used to clamp the median lobe dorso-ventrally just distal to the first pair. The second pair was then moved distally and the median lobe again clamped. This procedure was continued until the ostium was reached. The fluid pressure resulting from repeating clamping often everted the sac.

In some specimens fluid pressure was not sufficient to evert the internal sac. A pair of forceps was then inserted through the ostium, and the internal sac was pulled out. This procedure was more likely to damage the internal sac and was used only when the above technique failed.

In some specimens it was impossible to evert the internal sac by any method. This apparently was due to the beetle having been killed or stored in formalin or a strong alcohol solution.

Female genitalia on which the valvifer, stylus, and proctiger were to be examined were usually placed in a small container of water under a stereoscopic microscope and muscles or membrane obstructing the field of view were removed with forceps. Sometimes the genitalia were first placed in hot potassium hydroxide solution for 1 to 5 minutes to facilitate this removal.

Female genitalia in which the spermatheca was to be examined were placed in boiling or nearly boiling potassium hydroxide solution for approximately 1 minute. They then were transferred to a small dish of water and examined under a stereoscopic microscope. If the spermatheca was still obscured by muscles and other tissue, this treatment was repeated as needed. Care had to be employed since excessive clearing would render the spermatheca nearly transparent.

Genitalia vials were used to store: median lobes with everted internal sacs; female genitalia with cleared spermathecae; mouthparts; hindwings; and various other small structures. These vials are plastic with soft plastic stoppers. They prove superior to glass vials with cork stoppers since glycerine will not leak from them. The body part was placed in the vial with forceps and several drops of glycerine added with a syringe. The vial was then stoppered, and the pin supporting the specimen run through the stopper.

Most median lobes with internal sacs not everted and female genitalia with spermathecae not cleared were glued with clear nail polish to a small card or point pinned immediately beneath the specimens. Some median lobes were pierced with a minuten pin attached to a piece of polyporous pith pinned beneath the specimen.

Hind wings and mouthparts were removed from the specimens by grasping their bases with forceps and pulling the structures off the insect. The hind wings and mouthparts were then usually treated as follows. Each of these structures was first placed in a container of 95 percent ethanol and then placed in clear nail polish which was applied to a small card pinned immediately beneath the insect. The hind wings were completely unfolded so that all areas were visible, and the mouthparts were arranged so that the desired part of them was visible for examination. This procedure minimized shrinking of membranous structures and provided a simple method of preserving wings and mouthparts for ready viewing without the necessity of preparing slides. It also had the advantage of directly associating each structure with the specimen from which it was removed.

Measurements

On specimens employed in species revisions.

Total body length measurements were made for each species to give a general impression

of its size range. The 5 largest and 5 smallest specimens of each species were visually selected and measured as follows. The specimen being measured was placed sideways under a stereoscopic microscope with a calibrated ocular grid. The body length was measured along the side from the mandible apex to the abdominal apex. When the mandibles or abdomen of a specimen being measured were extended or retracted, the specimen was relaxed in hot water and the body parts arranged in normal position.

On specimens employed in supra-specific revisions.

Specimens were measured by the technique described above. However in many instances less than the 5 largest and 5 smallest specimens of each species were visually selected and measured.

Illustrations

Line drawings of morphological characters were made with the aid of a drawing tube on a Wild stereoscopic microscope. Unless otherwise noted, the accompanying scale lines equal 1 mm. Distribution maps of taxa were made by using dots to represent localities.

Some readers may be interested only in the species revisions presented here, in the supra-specific revisions, or in the discussions on phylogeny and zoogeography. Therefore the illustrations are placed in the following order at the end of the text: (1) drawings of morphological characters and species distribution maps of assistance in identifying North American species of *Anisotarsus*, *Notiobia* (s. str.), and *Gynandrotarsus*; (2) drawings of morphological characters of assistance in identifying supra-specific taxa; and (3) diagrams and maps referred to in the discussions on phylogeny and zoogeography.

Format

Each species or supra-specific description provides reference to: the original publication of the valid name of the taxon in the form in which this taxon was first published; and the original publication of each synonym in the form in which the synonym was first published. Many papers, especially regional checklists, are based on incorrectly identified material and therefore are of little value. Also the mere listing of references does not tell the reader what the reference said concerning the taxon. Such listing is better published in formal catalogues, such as the Csiki catalogue on Carabidae and the forthcoming revised carabid catalogues being prepared by T. L. Erwin, and is here omitted.

Taxonically important papers are reviewed in full in a discussion section under the appropriate taxon. This discussion section also contains information concerning problems with types and reasons for synonymy or proposed taxonomic changes.

Lists of individual localities from which specimens were seen and of the museums loaning the specimens are omitted. The individual distributional maps provide a good impression of the range of each species. Readers desiring these data or other additional information may contact me.

Sections on distribution and material examined are included with each species description. Where sufficient information is available, sections on variation, flight, and bionomics are also included. The section on variation discusses intra- and interpopulational variation. The section on bionomics summarizes all available information on a species' phenology, ecology, biology and feeding habits. Much of the information concerning ecology was kindly supplied by G. E. Ball; this information is referred to as "Ball's data" in the various sections. The section on distribution and material examined outlines the general distribution of each species and gives the number of specimens examined. It also provides information on disjunct populations of a species.

The discussion section of each genus or subgenus whose species are not revised in this pa-

per provides a list of the included species. The author and date of original publication are provided for each such species, but in most instances the original description is not listed in the references cited section. Readers desiring such bibliographic information may consult standard catalogues such as Csiki (1932). An asterisk immediately behind the date of a species indicates that I have not examined specimens of that species. An asterisk behind a male or female symbol indicates that I have not examined specimens of that sex of the species in question.

Abbreviations

The following abbreviations were used in the synonymy and discussion sections to identify museums containing type specimens:

BMNH	British Museum of Natural History, London, S.W. 7, Great Britain
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MNHP	Museum National d'Histoire Naturelle, 45 bis rue de Buffon, Paris (V), France
UASM	University of Alberta, Strickland Museum, Edmonton, Alberta
USNM	United States National Museum Smithsonian Institution, Washington, D.C.

Taxonomic Characters and Terminology

Color. — Body color is useful in distinguishing many taxa. Color is described with terms taken from Torre-Bueno (1962). Metallic tinges are frequently present on the dorsum and are often helpful in identification of taxa. Perception of such tinges is often affected by the type of light used, and the manner of illumination is therefore explained where appropriate.

Microsculpture. — Microsculpture is useful in characterizing some taxa. The primitive condition is that of an isodiametric mesh. Modifications encountered are: microsculpture reduced or absent; granulate; transversely stretched; consisting of fine transverse lines; and consisting of punctures. No matter what type of microsculpture is present, it is usually more prominent in female specimens. The microsculpture of some species appears composed of granulate mesh or of punctures depending on which angle light strikes the specimens. When the mesh is granulate, the flat areas between granulae appear as though punctured under certain lighting conditions.

Head. — The frontal fovea on each side of the head each bears a clypeo-ocular prolongation in some specimens. This prolongation (Fig. 46) appears as a groove or linear impression directed towards the general vicinity of the eye. When the fronto-clypeal suture joins the frontal fovea and ends there, the clypeo-ocular prolongation may appear to be a shallow continuation of this suture. The presence, absence, and degree of development of the clypeo-ocular prolongation are useful in distinguishing several taxa.

The presence, absence, and degree of development of a transverse suture between the mentum and submentum are useful in delimiting many taxa. In relatively plesiomorphic groups such as *Anisotarsus* the mentum and submentum are separated by a complete transverse suture which appears as a narrow transverse membranous band (Fig. 170). In most specimens of the genus *Progonochaetus* the suture is still visible medially but has disappeared laterally. In specimens of more apomorphic genera such as *Anisodactylus* the mentum and submentum have become completely fused and the former suture is at most indicated by a faint groove (Fig. 171). In dried specimens possessing a suture between the mentum and submentum, the suture may be shrunken and difficult to discern. Therefore the reader

should soak "doubtful" specimens in hot water for 2 to 3 minutes to make the suture more evident.

Abdomen. — The last visible sternum is referred to in descriptions as "sternum VI". This is the apparent sixth sternum and the morphological seventh sternum. The number of ambulatory setae on sternum VI of males is useful in separating some species. When only 1 pair is present, a single seta is placed on each side slightly laterad to the middle apex of the sternum. When 2 pairs are present, an additional seta is located on each side just lateral to the seta described above.

Most specimens of Anisodactylina have 1 pair of ambulatory setae on abdominal sterna III to V, 1 or 2 pairs on sternum VI, and patches of very short fine setae on sterna I and II under the trochanters and bases of the femora. When additional setae are present, they are referred to as "extra setae".

Male genitalia. — The median lobe of the male genitalia is frequently very important in separating species. The proximal enlarged bulb-like region which receives the basal orifice is referred to as the basal bulb. The portion between the basal bulb and the distal end of the dorsal membranous area is termed the shaft. And the portion between the distal end of the membranous dorsal area and the distal end of the median lobe is here called the apex. Frequently the apex is swollen distally producing a dorso-ventral thickening termed the apical disc. The parameres of males are fairly constant and do not offer readily apparent characters for defining taxa within the subtribe. The internal sac of the median lobe is useful in defining specific and supra-specific taxa in many groups of Carabidae. Within Anisodactylina, however the internal sac exhibits considerable intrapopulational variation and normally is of no assistance in delimiting species or even subunits of species.

Female genitalia. — The female genitalia provide useful characters for delimiting several supra-specific groups. There has been considerable disagreement among workers over homology and consequently also terminology of the structures of the female genitalia. Tanner (1927) studied the genitalia of female Coleoptera and concluded that: (1) the genitalia consist of the eighth, ninth and tenth abdominal segments and appendages; (2) the appendages of the eighth and tenth segments have disappeared; (3) the appendages of the ninth segment consist of the styli, coxites, and valvifers and are borne on the distal end of the ninth sternite; and (4) the proctiger forms part of the tenth tergite.

Lindroth and Palmen (1956) discussed the female genitalia of Coleoptera and Lindroth (1957) provided a table containing terms used by previous workers. Lindroth and Palmen (1956) concluded that the ninth sternum of female Coleoptera "as a rule is divided into a pair of "hemisternites" . . . between which the vulva . . . is situated. Each hemisternite usually bears an articulating process, the stylus . . .". The term "hemisternite" as used by Lindroth and Palmen (1956) refers to the same plate-like structure as does the "valvifer" of Tanner (1927). The basal segment of the structure termed the "stylus" by Lindroth and Palmen (1956) refers to the "coxite" of Tanner (1927). (Lindroth, 1957, mistakenly listed the term "coxites" of Tanner (1927) as being equivalent to the term "hemisternite"). The apical segment of the "stylus" of Lindroth and Palmen (1956) is equivalent to the "stylus" of Tanner (1927).

John Kingsolver kindly made available to me unpublished notes and drawings of R. E. Snodgrass which are stored at the Smithsonian Institution, Washington D. C. The notes and drawings refer to a dissection by Snodgrass of a species of the carabid genus *Pterostichus* (species not stated). These notes are quoted in part below to make them available to other workers and to hopefully assist in stabilizing the terminology of parts of the female genitalia. The drawings of Snodgrass are shown in Figs. 167, 168, 169.

"The normally exposed part of the abdomen ends with the seventh segment. From this

the eighth segment consisting of a narrower tergal and sternal plate is protractile. Beyond the eighth seg [sic] is a wide annulus of membrane (called IX seg. by Tanner), and beyond this the ninth segment bearing the pair of ventrolateral appendages. The tenth segment, a proctiger, is small and mostly concealed within the ninth seg.

"The two-segmented genital appendages are supported on each side by a prominent oval plate (a), the anterior end of which is broadly invaginated and of an apodemal nature. These plates Tanner calls the "valvifers". The proximal segment of the free part of the appendage (b) (the "coxite" of Tanner) is elongate, at the terminal segment (c) ("stylus" of Tanner) is a hook-like claw curved inward and outward.

"The genital appendage as a whole has little resemblance to an ordinary gonopod of an ovipositor. The supporting plate, however, has two muscles arising on the ninth tergum: one (1) a large oblique muscle, the other (2) a flat muscle with . . . fibers from edge of T to edge of plate a. The basal seg. of the appendage has a muscle (3) from . . . ventral surface of plate a to its proximal ventral extremity. The hook has two muscles, a large flat fan of fibers (4) arising on inner face of plate a, inserted on dorsal angle of its base, and a small muscle (5) arising proximally on b and having same insertion as 4. Evident that a belongs to IX seg. and that it may be the valvifer of this seg., but musculature of b and c have little resemblance to valvifer muscles of gonopophyses; though b + c may represent a two-segmented stylus. Since the valvifer is the "coxite", Tanners (sic) distinction between valvifer and "coxite" is not logical. If b, b are bases of appendages, then a, a do not represent the sternum of IX seg. (as supported by Tanner), since the latter would lie between the appendages."

These notes of Snodgrass suggest that the 2 segmented structure ("b + c" of Fig. 167) is best termed the "stylus". And since the plate-like structure supporting the stylus ("a" of Fig. 167) may represent the valvifer, it seems best to term it "valvifer" rather than accept the additional term "hemisternite" proposed by Lindroth and Palmen (1956).

SYSTEMATICS

The Subtribe Anisodactylina

Anisodactylides Lacordaire, 1854: 257, 268
 Anisodactylites Jacquelin du Val, 1857: 35, 64
 Anisodactyli G. Horn, 1881: 176, 184
 Anisodactylinae H. W. Bates, 1882: 49
 Anisodactylidae Peringuey, 1896: 417
 Anisodactylini Tschitscherine, 1900: 344, 351, 367
 Anisodactylina Jakobson, 1907: 370
 Anisodactylitae Jeannel, 1942: 600

Diagnosis. — Head with 1 seta over each eye. Mandible lacking seta in scrobe. Antenna inserted on side of head directly between eye and base of mandible; segments III to XI or IV to XI covered with setae or pubescence; segments I to II or I to III with rings of setae at apex only. Mentum (except in *Rhysopus*) with 1 seta on each side of median area. Ligula with 2 distal ventral setae and lacking additional setae except in *Scybalicus*, *Pseudanisotarsus*, and *Progonochaetus*. Labial palp with penultimate segment plurisetose on anterior margin; terminal segment subequal in size to penultimate segment, not minute. Forecoxal cavity closed and uniperforate. Midcoxal cavity entirely enclosed by sterna, mesepimeron not reaching midcoxal cavity. Foretibia with inner spur terminal, outer spur subapical; both spurs more or less associated with antennal cleaner. Foretarsus of ♂ (except in some *Progonochaetus (Eudichirus) jeanneli* [R. Clarke, personal communication] and in some *Dicheirus dilatatus angulatus*) with segments I to IV or II to IV laterally expanded and

spongy pubescent beneath. Midtarsus of ♂ also modified in most species. Scutellum of mesothorax normally exposed. Elytron with basal bead extending to or just short of scutellum; lacking epipleural plica at apex. Abdomen normally with 6 visible sterna. Median lobe when symmetrical with distal portion of shaft containing ostium not deflected to the left; basal bulb well developed; in most species shaft immediately distal to basal bulb bent and giving arcuate shape to median lobe. Parameres short and broad, conchoid, or oviform; similar in shape except right one always smaller; lacking setae.

Description. Body length 6.3 to 19 mm. Body form various.

Color. Body generally rufopiceous to black, with brighter colors or metallic tinges in some taxa.

Head. Labral apex straight to strongly emarginate medially. Clypeus with apex straight to prominently emarginate medially, with 1 long seta at each outer distal angle unless otherwise stated. Eye small to large. Frons with varied fovea; microsculpture usually of isodiametric mesh. Mentum with or without tooth situated medially on distal margin of mentum; except for *Rhysopus* (which lacks setae) with 1 seta on each side of median area of apex, when tooth present such seta situated at lateral base of tooth. Mentum and submentum separated by a complete transverse suture (Fig. 170) or fused laterally but still separated medially; or completely fused (Fig. 171). Submentum of all taxa except *Phanagnathus overlaeti* with 1 long inner and 1 short outer seta on each side, in *Phanagnathus overlaeti* with 1 long seta on each side. Ligula with 2 distal ventral setae and lacking additional setae except in *Pseudanisotarsus*, *Progonochaetus*, and *Scybalicus hirtus*. Paraglossa membranous and glabrous unless otherwise stated. Penultimate segment of labial palp plurisetose on anterior margin.

Thorax. Pronotum of various shapes; 1 long seta on lateral margin near mid point except 2 lateral setae on each side in *Progonochaetus* and *Diachromus*; apical bead present at least laterally except in *Dicheirus*; microsculpture various, but of isodiametric mesh in most specimens. Apex of prosternal lobe with several prominent setae.

Legs. Foretarsus of all ♂♂ and midtarsus of most ♂♂ with segments I to IV or II to IV laterally expanded and with ventral spongy pubescent vestiture except in some ♂♂ of *Progonochaetus (Eudichirus) jeanneli* [R. Clarke, personal communication] and of *Dicheirus dilatatus angulatus*.

Elytron. Humerus with or without tooth; scutellar stria unless otherwise noted short and arising from near base of stria II and with ocellate puncture near its base; intervals flat to convex, with or without setigerous and non-setigerous punctures; subapical sinuation various; microsculpture various but of isodiametric mesh in most specimens.

Hind wing. Full in most species but vestigial or varied from full to vestigial in some species.

Abdomen. Sterna III to V each with 1 pair of ambulatory setae, with extra setae in some taxa; sternum VI of ♀ with 2 pairs of ambulatory setae, except genus *Allocinopus* with only 1 pair such setae; sternum VI of ♂ with 1 or 2 pairs of ambulatory setae.

Male genitalia. Median lobe arcuate and symmetrical in most species (except arcuate and asymmetrical in *Notobia tucumana* and *Xestonotus lugubris*, twisted distally in *Dicheirus piceus*, and *Anisodactylus binotatus*, only slightly arcuate in species of the subgenus *Pseudohexatrichus*); membranous area of dorsum various; apical disc present or absent; venter sclerotized, except membranous in 1 species of genus *Allocinopus*. Parameres short and broad, conchoid or oviform, right similar to left but smaller.

Female genitalia. Valvifer various in shape, degree of sclerotization, and distal pubescence. Stylus with 2 segments, segments fused in *Pseudanisodactylus*; unless otherwise noted basal segment lacking setae and distal segment with 2 distal setae on mesal margin and with lateral

margin excavate (Fig. 237). Proctiger in most species consisting of irregular semi-sclerotized area with stout setae on each side of anus. Spermatheca (Fig. 128) tubular with distal portion annulated (distal annulated portion shorter in some species than shown in Fig. 128).

Internal organs. Rectum with 2 rows of oval rectal glands, 3 glands in each row.

Discussion

Anisodactylina like other subtribes of Harpalini has been differently defined by various authors, primarily because those authors studied only those Anisodactylines from specific regions of the world. Rather than spend needless pages detailing past misconceptions concerning the subtribe, I shall concentrate on discussing the subtribe as defined in this paper.

The subtribe Anisodactylina is here defined to include all those Harpaline genera which agree with the diagnosis given earlier. Twenty four genera of Harpalines clearly fit this diagnosis and are regarded as members of the subtribe Anisodactylina. The genus *Smirnovia* Lutshnik, 1922 was described by Lutshnik (1922) for the single species *tristis* Lutshnik, 1922 from Turkestan. Lutshnik (1922) declared *Smirnovia* to be closely related to the genus *Anisodactylus* because of the similar general habitus of *Smirnovia tristis* and *Anisodactylus (A.) binotatus*. Schauberger (1926) listed *Smirnovia* as a member of Anisodactylina, and subsequent workers have accepted this placement. I have not been able to examine specimens of *Smirnovia tristis*, but I have read the original description of this taxon. According to the original description, *Smirnovia tristis* has 2 supra-orbital setae over each eye; all other members of the tribe Harpalini have only a single such seta over each eye. Probably the genus *Smirnovia* belongs in a different tribe. Until specimens of *Smirnovia* can be examined, the genus is best treated as *incertae sedis* within the tribe Harpalini.

Basilewsky (1950) included *Anisochirus* Jeannel, 1946 as a valid genus belonging to Anisodactylina. This genus was described by Jeannel (1946) as monotypic, containing only the species *alluaudi* based on a single male from Madagascar. Basilewsky (1950) noted that *Anisochirus alluaudi* differed from all other African and Madagascar Anisodactylines by having the distal portion of the median lobe containing the ostium deflected to the left as in species of *Harpalus*. Quite possibly Basilewsky was not able to examine the holotype of *Anisochirus alluaudi* since his descriptions of the genus and species are quite short, and his drawing of the median lobe of *alluaudi* looks like a redrawing of that provided by Jeannel (1948).

George E. Ball kindly examined the holotype of *alluaudi* at the MNHP and supplied the following information. The median lobe indeed did have the distal portion containing the ostium deflected to the left. The holotype was glued to a card which made examination of the tarsal vestiture difficult. Removal of the holotype from the card revealed that the tarsal vestiture was biseriate as in *Harpalus*. And the holotype keyed out in Basilewsky (1950, 1951) to *Harpalus madagascariensis* Dejean, 1831 which was cited by Basilewsky (1951) as being common throughout Madagascar. Comparison with identified specimens of *madagascariensis* indicated that *alluaudi* is a junior synonym of that species (NEW SYNONYMY), and thus that *Anisochirus* is congeneric with *Harpalus* (NEW SYNONYMY).

The monotypic genus *Xenophonus* G. Müller, 1942 was treated as a member of Anisodactylina by Basilewsky (1950) who apparently saw only female specimens of *X. hirtus* G. Müller, 1942. I have examined the male holotype of *X. hirtus* and found that: the foretarsus has the apex of segment I and all of segments II to IV moderately expanded laterally and biseriate beneath; the elytron is iridescent; and the ostium of the median lobe is dorsal in position. Because of this combination of characters, *X. hirtus* and the genus *Xenophonus* are not members of the subtribe Anisodactylina and are here transferred to the Selenophori group of the subtribe Harpalina.

I believe that the 24 genera examined by me and treated as members of Anisodactylina constitute a monophyletic group. However it is not possible to state that the subtribe is defined on the basis of clearly apomorphic character states. The main features defining the subtribe are: penultimate segment of labial palp plurisetose on anterior margin; ventral vestiture of male fore- and midtarsi spongy pubescent; median lobe with distal portion of shaft containing ostium not deflected to the left. The unmodified form of median lobe would seem to be a plesiomorphic feature within the tribe Harpalini. Spongy pubescent tarsal vestiture is restricted to Anisodactylina and the sub-tribe Pelmatellina and is probably apomorphic. The plurisetose condition of the penultimate segment of the labial palp may or may not be apomorphic.

If spongy pubescent tarsal vestiture is indeed apomorphic, then the subtribe Pelmatellina is the sister group of Anisodactylina. Species of Pelmatellina possess the spongy pubescent tarsal vestiture found in Anisodactylina but differ from species of that subtribe by having 2 or 3 setae on the anterior margin of the penultimate segment of the labial palp. In addition, species of at least the Pelmatelline genera *Nemaglossa*, *Pelmatellus*, and *Thenarellus* differ from species of Anisodactylina by lacking setae at the apex of the prosternal lobe (personal communication from H. Goulet who is revising supra-specific taxa of Pelmatellina – other 2 genera of that subtribe not yet examined for presence or absence of setae).

Further elucidation of the plesiomorphy and apomorphy of the characters defining Anisodactylina will have to wait until the other 6 subtribes of Harpalini have been revised on a world-wide basis.

Key to the Genera and Subgenera of the Subtribe Anisodactylina

Notes concerning the key

The 37 supra-specific taxa of which I have seen specimens are separated in the key below. The number of pronotal lateral setae is used as a separating character in the first couplet. The pronotal lateral setae are more elongate than any other pronotal pubescence and therefore easily discerned even on densely pubescent specimens. When the pronotal lateral setae are broken off, their number can still be determined by careful examination since each such seta arises from a socket slightly larger than that associated with other pronotal pubescence.

Key to the Genera and Subgenera of the Subtribe Anisodactylina

1	Pronotum with 2 lateral setae on each side (in most specimens anterior seta located before or in midregion of lateral margin and posterior seta located in region of posterior angle)	2
–	Pronotum with 1 lateral seta on each side (such seta situated in midregion of lateral margin)	4
2 (1)	Dorsum tricolored, head and base of elytron rufotestaceous, pronotum black, apex of elytron violaceous or bluish brown; range England, Europe, Mediterranean area	<i>Diachromus</i> Erichson, p. 381
–	Dorsum not so colored, rufopiceous to black; range Madagascar and Africa south of the Sahara Desert	3
3 (2)	Pronotum (Fig. 187) with side sinuate before acute, outward projected posterior angle	<i>P. (Eudichirus)</i> Jeannel, p. 343
–	Pronotum (Figs. 184, 186) with side not sinuate and posterior angle not acute and outward projected	<i>P. (Progonochaetus)</i> G. Müller, p. 342
4 (1)	Mentum and submentum separated by complete transverse suture (Fig. 170)	5
–	Mentum and submentum completely fused (Fig. 171)	18
5 (4)	Body (except part of elytron in some specimens) with dense pubescence ..	6

—	Body without dense pubescence	7
6 (5)	Pronotum suborbiculate (Fig. 181); clypeal apex raised into bead; range Africa to India	<i>Crasodactylus</i> Guerin-Meneville, p. 286
—	Pronotum semi-cordate (Fig. 183); clypeal apex not raised into bead; range England, Europe, Mediterranean area	<i>Scybalicus</i> Schaum, p. 339
7 (5)	Pronotum (Fig. 180) suborbiculate; AND lateral depression prominently flattened and sharply delimited from convex disc by discrete groove; AND apex of ligula not expanded laterally; AND abdominal sternum VI of ♀ with distal margin enlarged medially as plate-like area in posterior view (Fig. 205); range Australia	<i>Cenogmus</i> Sloane, p. 287
—	Pronotum various in shape; pronotal lateral depression various, if sharply delimited from convex disc then apex of ligula broadly expanded laterally and pronotum cordate; abdominal sternum VI of ♀ unmodified	8
8 (7)	Pronotal disc pubescent at least along lateral part of apex; abdominal sterna with extra setae; range temperate southern South America	9
—	Pronotal disc glabrous except for single lateral seta on each side; extra setae on abdominal sterna present or absent; range New World, and Australian Region	10
9 (8)	Ligula with apex narrow, not laterally expanded, and with dorsum bearing 4 to 5 distal setae; pronotum not strongly cordate, lateral depression not sharply delimited; pronotal pubescence extended along lateral portions of basal and apical margins and along side; elytral intervals I, III, V, and VIII each with row of dorsal setigerous punctures	<i>Pseudanisotarsus</i> new genus, p. 290
—	Ligula with apex strongly expanded laterally and dorsum lacking setae; pronotum strongly cordate and with lateral depression broadly concave and sharply delimited from disc; pubescence on pronotum restricted to lateral part of apex; odd and in some specimens also even elytral intervals each with irregular row of non-setigerous punctures	<i>Criniventer</i> van Emden, p. 292
10 (8)	Body depigmented, testaceous in color; body length 9.5 mm or less; range New Zealand	<i>Triplosarus</i> H. W. Bates, p. 285
—	Body not depigmented, rufopiceous to black or metallic in color; body length often more than 9.5 mm; range Australian Region (including New Zealand), New World, Africa	11
11 (10)	Third and often other elytral intervals with 3 or more dorsal setigerous punctures (such punctures frequently extended to basal area of elytron)	12
—	Third elytral interval with 1 or 2, dorsal setigerous punctures	13
12 (11)	Frontal fovea of head lacking clypeo-ocular prolongation; median lobe lacking apical disc; range Australian Region and eastern part of Oriental Region	<i>Gnathaphanus</i> MacLeay, p. 289
—	Frontal fovea of head with clypeo-ocular prolongation (may be faint); median lobe with button-like apical disc (Figs. 210, 211); range Ethiopian Region	<i>N. (Diatypus)</i> Murray, p. 337
13 (11)	Pronotum cordate and with side sinuate before posterior angle; AND gena wide, narrowest part of gena between mouth and eye as wide or wider than maximum width of first antennal segment; AND dorsum without metallic tinges; abdominal sternum VI of ♂ with 1 pair of ambulatory setae; range New Zealand	<i>Allocinopus</i> Broun, p. 284
—	Pronotum not cordate and side not sinuate before posterior angle; OR if pronotum cordate and side sinuate then gena narrow with narrowest part between	

mouth and eye much narrower than maximum width of first antennal segment; OR dorsum with metallic tinges, abdominal sternum VI of ♂ with 2 pairs of ambulatory setae; range Australian Region (including New Zealand) and New World 14

14 (13) Abdominal sterna with extra setae (such setae may be very short and fine); AND mental tooth present; AND hindtarsus stout with first segment approximately twice as long as wide and always shorter than II + III; range Australian Region and as far towards Eurasia as Sumatra and Java *Hypharpax* MacLeay, p. 388

— Abdominal sterna lacking extra setae; OR mental tooth absent; hindtarsus of most specimens not stout; range Australian Region, and New World 15

15 (14) Gena narrow, at narrowest point narrower than maximum width of first antennal segment; OR frontal fovea of head with clypeo-ocular prolongation; eye of most specimens large and protruding 16

— Gena wide, at narrowest point wider than maximum width of first antennal segment; frontal fovea of head lacking clypeo-ocular prolongation; eye of most specimens not large and protruding; range New World and Australian Region *N. (Anisotarsus)* Chaudoir, p. 295

16 (15) Frontal fovea of head with clypeo-ocular prolongation; range tropical and subtropical areas of the New World *N. (Notiobia)* Perty, p. 321

— Frontal fovea of head lacking clypeo-ocular prolongation 17

17 (16) Frontal fovea of head large, prominent; supra-antennal ridges strongly divergent anteriorly from eyes; eye large and protruding; range tropical and subtropical areas of the New World *N. (Notiobia)* Perty, p. 321

— Frontal fovea of head small, not prominent; supra-antennal ridges various, in most specimens not strongly divergent anteriorly from eyes; size of eye various; range temperate areas of the New World but extending along mountains into tropical and subtropical areas and also present in the Australian Region *N. (Anisotarsus)* Chaudoir, p. 295

18 (4) Foretibia (Fig. 195) with apical portion strongly expanded laterally and with large excavate dilation at external apex; head with preocular sulcus receiving first antennal segment when in repose; range eastern North America *Geopinus* LeConte, p. 377

— Foretibia with apical portion not strongly expanded laterally and without large excavate dilation at external apex; head lacking preocular sulcus 19

19 (18) Dorsum, including all of elytron, densely pubescent 20

— Dorsum mainly glabrous, elytron at most pubescent along margins 24

20 (19) Dorsum tricolored with head and pronotum black; base of elytron rufotestaceous; apex of elytron violaceous brown; AND foretibial apical spur trifid (Fig. 45); range Europe, Mediterranean area, Syria, Transcaspian *Gynandromorphus* Dejean, p. 380

— Combination of morphological characters not as above 21

21 (20) Pronotal apical bead absent; foretibial apical spur trifid (Fig. 45); range western North America *Dicheirus* Mannerheim, p. 381

— Pronotal apical bead present at least laterally; foretibial spur lanceolate (Fig. 188) or angulately swollen at sides (Fig. 189) 22

22 (21) Ligula apex not expanded laterally (Fig. 178); dorsum with head and pronotum testaceous to rufotestaceous, elytron piceous and strongly iridescent due to microsculpture of extremely fine dense lines; range eastern North America

..... *A. (Amphasia)* Newman, p. 380

— Ligula apex expanded laterally (Fig. 177); dorsum not colored as above; elytron of some specimens with metallic tinges but microsculpture always of isodiametric mesh 23

23 (22) Dorsum dull black, lacking metallic tinges; AND pronotum with side evenly rounded from apex to base and basal impression shallow and not separated from lateral margin by a convexity; range eastern North America
..... *A. (Pseudamphasia)* Casey, p. 379

— Dorsum with metallic tinges OR partly testaceous to rufotestaceous; OR pronotum with side sinuate before posterior angle OR with prominent linear basal impression separated from lateral margin by a convexity
..... *A. (Anadaptus)* Casey, p. 373

24 (19) Pronotum with lateral depression abruptly set off from convex disc by prominent inflexion of integument in apical 4/5 (frontispiece); elytral stria sharp, semi-rectangular in section; dorsum with metallic green or aeneous tinge; range eastern United States *A. (Pseudaplocentrus)* new subgenus, p. 377

— Pronotum lacking such inflexion of integument; elytral stria rounded in section, not extremely sharp; dorsum with or without metallic tinge 25

25 (24) Dorsum bicolored, head and base of elytron rufotestaceous, pronotum and median and apical portions of elytron bluish black; range Europe, Mediterranean area *A. (Pseudhexatrichus)* new subgenus, p. 352

— Dorsum not colored as above 26

26 (25) Frontoclypeal suture extremely deep, obliterating frontal fovea and continuing posterio-laterally towards eye as very deep clypeo-ocular prolongation; AND mentum lacking tooth and setae; range Java, Sumatra, Indochina
..... *Rhysopus* Andrewes, p. 347

— Frontoclypeal suture not extremely deep; AND mentum with or without median mental tooth, bearing 1 seta on each side of median area 27

27 (26) Pronotum with broadly rounded posterior angle; AND dorsum covered with fine nonsetigerous punctures; AND microsculpture obsolescent or absent dorsally; range Sumatra, Philippines, Indochina, Japan
..... *Harpalomimetes* Schauberger, p. 346

— Combination of morphological characters not as above 28

28 (27) Ligula narrow with apex not expanded (Fig. 175) 29

— Ligula broader with apex expanded laterally (Figs. 176, 179) 32

29 (28) Third elytral interval with 3 to 6 setigerous punctures in row from apex to or nearly to base; AND mentum with median tooth; range temperate southern South America *Anisostichus* van Emden, p. 338

— Third elytral interval with at most 2 setigerous punctures, not with row from apex to base; OR mentum lacking median tooth 30

30 (29) Mentum with prominent long median tooth (Fig. 172); range Oriental Region, Tibet, China, Japan, and extending as far towards Australia as New Guinea
..... *Chydaeus* Chaudoir, p. 345

— Mentum lacking tooth 31

31 (30) Frontal fovea of head bearing prominent clypeo-ocular prolongation; segments II to IV of hindtarsus of both sexes and segments II to IV of fore- and mid-tarsus of ♀ with dense ventrolateral cover of somewhat thickened setae; median lobe of ♂ symmetrical; range Madagascar and Oriental Region
..... *Pseudognathaphanus* Schauberger, p. 344

Frontal fovea of head lacking clypeo-ocular prolongation; tarsi lacking dense ventro-lateral cover of somewhat thickened setae; median lobe of ♂ asymmetrical (Figs. 212, 213); range eastern North America *Xestonotus* LeConte, p. 347

32 (28) Mentum with prominent long median tooth (Fig. 172); dorsum of mandible not striate; range Oriental Region, Tibet, China, Japan, extending as far towards Australia as New Guinea *Chydaeus* Chaudoir, p. 345

— Mentum lacking tooth or if tooth present then not prominent; AND/OR dorsal apex of mandible striate 33

33 (32) Foretibial apical spur lanceolate (Fig. 188), swollen laterally (Fig. 189), or in a few specimens of *Anadaptus* subtrifid (190), not trifid 38

— Foretibial apical spur trifid (Fig. 45) 34

34 (33) Clypeus with 1 seta at each outer distal angle 35

— Clypeus with 2 or more setae at each outer distal angle 37

35 (34) Pronotal lateral base including basal fovea covered with small dense non-setigerous punctures; elytron of some specimens also covered with small dense non-setigerous punctures; valvifer of ♀ triangular and with distal setae (Fig. 218); range Korea, Japan, China, India, Burma, Indochina *A. (Anisodactylus)* Dejean, p. 349

— Pronotal lateral base not covered with small dense non-setigerous punctures (basal fovea may however have a few scattered small non-setigerous punctures; elytron not covered with small dense non-setigerous punctures; valvifer of ♀ subtriangular and lacking distal setae (Figs. 130, 220) 36

36 (35) Hindtarsus with segment I as long as or longer than II + III; valvifer of ♀ with concave area along distal margin (Fig. 130); range North America *A. (Gynandrotarsus)* LaFerté, p. 354

— Hindtarsus with segment I shorter than II + III; valvifer of ♀ lacking concave area along distal margin (Fig. 220); range Mediterranean area *A. (Pseudodichirus)* Lutshnik, p. 354

37 (34) Foretibia of ♂ with inner proximal basal margin strongly and abruptly emarginate (Fig. 192); dorsum of many specimens with metallic tinge; valvifer of ♀ subtriangular and with truncate apex (Fig. 222); range England, Europe to Norway and southern Russia, Balkan Peninsula, and Mediterranean area *A. (Hexatrichus)* Tschitscherine, p. 353

— Foretibia of ♂ with inner proximal basal margin not strongly and abruptly emarginate (Figs. 193, 194); dorsum without metallic tinge; valvifer of ♀ triangular (Figs. 217, 218); range eastern North America *A. (Anisodactylus)* Dejean, p. 349

38 (33) Body with short semicordate pronotum and long parallel sided elytra; AND mandible prolonged with striate dorsal surface; AND labral apex strongly emarginate medially; range eastern North America *A. (Spongopus)* LeConte, p. 374

— Combination of morphological characters not as above 39

39 (38) Body broad and *Amara*- like and with metallic greenish, aeneous, bronze, or bluish tinges on dorsum *A. (Aplocentrus)* LeConte, p. 375

— Body not broad and *Amara*- like and lacking dorsal metallic tinges 40

40 (39) Hindtarsus stout with segment I shorter than II + III 41

— Hindtarsus not stout and with segment I equal to or longer than II + III 42

41 (40) Body of most specimens narrow and subcylindrical; outer distal angle of clypeus

of many specimens with 2 or more setae; dorsum of many specimens with rufotestaceous or metallic tinged areas; median lobe of ♂ with button-like apical disc (Figs. 206, 207); valvifer of ♀ various but never triangular in form, with or without distal setae; range North America *A. (Anadaptus)* Casey, p. 373

— Body not narrow and subcylindrical; outer distal angle of clypeus with 1 seta; dorsum piceous to black, never with rufotestaceous or metallic tinged areas; median lobe of ♂ lacking apical disc; valvifer of ♀ triangular (Figs. 217, 218) or lobed (Fig. 221) in form and with distal setae 42

42 (40, 41) Entire dorsum densely covered with small nonsetigerous punctures; valvifer of ♀ with distal setae, triangular or lobed in shape; (Figs. 217, 218, 221); range Eurasia and North America 43

— Entire dorsum not densely covered with small non-setigerous punctures; valvifer of ♀ with distal setae and triangular in shape (Figs. 217, 218); range North America and Eurasia excluding Japan, Korea and tropical Asia *A. (Anisodactylus)* Dejean, p. 349

43 (43, 42) Third elytral interval bearing dorsal setigerous puncture near middle or apical 1/3 (puncture and setae on some specimens small and difficult to discern at magnifications less than 50x); valvifer of ♀ triangular in shape (Figs. 217, 218); range North America and Eurasia excluding Japan, Korea and tropical Asia *A. (Anisodactylus)* Dejean, p. 349

— Third elytral interval lacking dorsal setigerous puncture; valvifer of ♀ lobed in shape (Fig. 221); range Japan, Korea and China *A. (Pseudanisodactylus)* new subgenus, p. 351

1 genus *Allocinopus* Broun

Allocinopus Broun, 1903: 607. [TYPE SPECIES: *Allocinopus sculpticollis* Broun, 1903, by monotypy].

Description. — Body length 6.3 to 11.3 mm. Body relatively elongate.

Color. Body rufopiceous to black, no metallic tinge on dorsum.

Head. Labral apex slightly to moderately emarginate medially. Clypeus with apex straight to prominently emarginate, when prominently emarginate exposing base of labrum in many specimens. Eye normal to very small. Frons with fovea punctiform; microsculpture of isodiametric mesh, obsolescent medially in some specimens. Mentum with prominent tooth. Mentum and submentum separated by complete transverse suture. Ligula narrow, not expanded at apex. Paraglossa, slightly longer than ligula.

Thorax. Pronotum cordate; lateral and basal beads complete; apical bead present laterally; microsculpture of isodiametric mesh or obsolete. Metepisternum wider than long.

Legs. Foretibia with distal portion slightly expanded laterally; apical spur lanceolate or slightly swollen basally. Hindfemur with 2 long setae on posterior margin. Hindtarsus with segment I shorter than II + III. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with apex of segment I in most specimens and all of segments II to IV in all specimens laterally expanded and spongy pubescent beneath.

Elytron. Humerus with or without small tooth; scutellar stria arising from base of stria II, with or without ocellate puncture at base, short or elongate and joined distally to distal portion of stria I, or in some specimens elongate and capturing distal portion of stria I and with basal portion of stria I short and appearing to be the scutellar stria; intervals flat to very slightly convex; interval III with or without dorsal setigerous puncture on apical 1/3 or 1/4;

microsculpture of isodiametric mesh, transverse mesh, or obsolete.

Hind wing. Vestigial.

Abdomen. Sterna III to V with extra setae in some ♂♂; sternum VI with 1 pair of ambulatory setae in both sexes.

Male genitalia. Median lobe with membranous area of dorsum short, not reaching basal bulb; apical disc absent; venter of shaft membranous in species labeled as *latitarsis*, sclerotized in other species.

Female genitalia. In *castaneus* and *angustulus* valvifer stylus, and proctiger absent and ovipositor consisting of membranous extension of vagina. In *sculpticollis* valvifer moderately sclerotized, not vestigial or absent, with 1 or 2 distal setae; stylus unmodified except basal segment with 2 seta at distal lateral margin; proctiger unmodified. Spermatheca unmodified in all species in which females were examined.

Discussion. — Csiki (1932) listed 5 species in this endemic New Zealand genus: *angustulus* Broun, 1912; *castaneus* Broun, 1912; *ocularis* Broun, 1908; *sculpticollis* Broun, 1903; *smithi* Broun, 1912. I have not examined specimens of *ocularis* or *smithi*. The BMNH contains a series of male specimens labeled as "*Allocinopus latitarsis*". I have not located a published description of an *Allocinopus latitarsis* nor have I found a species, in another genus, which might have provided the specific name for these specimens. The specimens labeled as *latitarsis* seem to agree well with the original description of *smithi* and may be members of that species. The species of *Allocinopus* are in need of revision.

The species in this genus exhibit variation in 3 characters normally stable enough to be used in defining genera and to a lesser degree subgenera. The external female genitalia (valvifer, stylus, and proctiger) are absent in *castaneus* and *angustulus* (or at least not visible at 120 magnification) and present in *sculpticollis* (females of other species not seen). The median lobe of a species labeled as *latitarsis* (see above) has the venter membranous between the basal bulb and apex while the median lobe of other examined species has the venter completely sclerotized. Lastly, many males of *sculpticollis* have extra setae on abdominal sterna III to V.

Despite these differences the genus appears to be a discrete monophyletic unit defined by the following character combination (*indicates character clearly apomorphic) eye small or almost vestigial*; mentum with prominent tooth and separated from submentum by complete transverse suture; ligula narrow; metepisternum wider than long; sternum VI of female with only 1 pair of ambulatory setae (Sternum VI has 2 pairs in females of all other genera in subtribe)*; and median lobe with membranous area of dorsum short and not extended to basal bulb.

2 genus *Triplosarus* H. W. Bates

Triplosarus H. W. Bates, 1874: 270. [TYPE SPECIES: *Triplosarus fulvescens* H. W. Bates, 1874, by monotypy].

Description. — Body length approximately 9 mm. Body rather stout.

Color. Body testaceous.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex straight or slightly emarginate. Frons with small punctiform fovea; microsculpture of isodiametric mesh. Mentum with prominent median tooth. Mentum and submentum separated by complete transverse suture. Ligula moderately wide but not laterally expanded at apex. Paraglossa slightly longer than ligula.

Thorax. Pronotum cordate; posterior angle prominent but rounded; lateral and basal beads complete; apical bead present laterally; microsculpture of isodiametric mesh or in

some specimens slightly stretched medially.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindfemur with 5 to 10 long setae on posterior margin. Hindtarsus with segment I approximately = to segment II and shorter than II + III.

Elytron. Intervals flat; interval III with dorsal setigerous puncture about 1/3 from apex; microsculpture of isodiametric mesh.

Hind wing. Full and apparently functional.

Abdomen. Sterna III to VI with numerous extra setae; sterna III to V with 1 pair of ambulatory setae each; sternum VI with 2 pairs of ambulatory setae. Tergum VIII of ♀ with broadly rounded apex.

Male genitalia. Median lobe with apex long, arising from right side and therefore slightly asymmetrical; membranous area of dorsum short, not reaching basal bulb; apical disc absent.

Female genitalia. Valvifer weakly sclerotized. Stylus weakly sclerotized and somewhat lobe like. Proctiger without normal setae but with many irregularly sclerotized plates.

Discussion. — Csiki (1932) lists 2 species in this endemic New Zealand genus: *fulvescens* Bates, 1874; and *novaehollandiae* (Castelnau), 1867. I have not been able to secure specimens of the latter species but suspect from its original description that it may be conspecific with *fulvescens*.

3 genus *Crasodactylus* Guérin-Méneville
(Fig. 181)

Crasodactylus Guérin-Méneville, 1847: 258. [TYPE SPECIES: *Crasodactylus punctatus* Guérin-Méneville, 1847, by monotypy].

Description. — Body length approximately 7.5 to 10 mm. Body with short moderately dense pubescence.

Color. Body black to dark piceous.

Head. Labral apex moderately to strongly emarginate medially. Clypeus with apex straight to slightly emarginate medially; raised transverse ridge present behind apex. Frons with fovea in *punctatus* punctiform and in many specimens fovea obscured by mainly non-setigerous punctures, in *indicus* fovea punctiform with clypeo-ocular prolongation and also in many specimens fovea obscured by mainly non-setigerous punctures; microsculpture obsolete. Antenna short, scarcely reaching pronotal base. Mentum without tooth or with slight median swelling in *punctatus*, with tooth in *indicus*. Mentum and submentum separated by complete transverse suture. Ligula narrow, not laterally expanded at apex. Paraglossa longer than ligula and curving behind it distally; dorsum and sides with moderately long pubescence.

Thorax. Pronotum (Fig. 181) suborbiculate in form, convex; posterior angle broadly rounded; lateral depression narrow; lateral and basal beads complete; apical bead present laterally; microsculpture obsolete.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindfemur with 2 long and various numbers of short setae on posterior margin. Hindtarsus with segment I shorter than II + III. Dorsum of all tarsi pubescent. Foretarsus of ♂ with apex of segment I in many specimens and all of segments II to IV in all specimens laterally expanded and spongy pubescent beneath. Midtarsus of most ♂♂ with segments II to IV slightly expanded laterally and each with patch of ventral spongy pubescence.

Elytron. Intervals slightly convex; moderately dense setigerous punctures covering surface in *punctatus*; setigerous punctures sparse and irregular on median portion but moderately dense on base, sides, and apex in *indicus*; microsculpture obsolescent except for irregular

weak isodiametric mesh apically.

Abdomen. Sterna with short dense pubescence; sternum VI of ♂ with 2 pairs of ambulatory setae; sternum VI of ♀ with median portion of apex slightly swollen as small plate-like disc somewhat as in *Cenogmus*.

Male genitalia. Median lobe with small apical disc.

Female genitalia. Valvifer strongly sclerotized and with several fine short distal setae; distal lateral margin deeply emarginate. Stylus with several fine short setae present proximally on apical segment. Proctiger on each side modified into sclerotized paddle-like structure free distally from tergum and with stout setae apically and laterally.

Discussion. — I have examined both sexes of the two species in the genus. The species *punctatus* Guerin-Meneville, 1847 inhabits sandy areas from western India south to the mountains of Kivu in the Belgian Congo and is also present on the Arabian peninsula (Andrewes, 1933; Basilewsky, 1950). The species *indicus* Andrewes, 1933 is cited in the original description as being found at several localities in western India.

4 genus *Cenogmus* Sloane
(Figs. 174, 180, 205, 232, 238)

Cenogmus Sloane, 1898: 456, 457, 460. [TYPE SPECIES *Cenogmus castelnau* Csiki, 1932: 1053, here designated, Csiki's replacement name for *Harpalus rotundicollis* Castelnau, 1867, preoccupied at time of original description by several other species in *Harpalus* named "rotundicollis"].

Description. — Body length approximately 8 to 10 mm. Body narrow and convex.

Color. Body rufopiceous to piceous.

Head. Labral apex moderately emarginate medially. Clypeal apex straight to moderately emarginate medially. Frons with fovea punctiform to elliptical, always small and with clypeo-ocular prolongation and in many specimens also with medio-posterior prolongation; microsculpture of isodiametric mesh. Gena wide, narrowest part between eye and mouth wider than maximum width of first antennal segment. Mentum without indication of a tooth in most specimens, some specimens with margin slightly swollen medially. Mentum separated from submentum by a complete transverse suture. Ligula elliptical in form and not expanded at apex (Fig. 174); side with small concave area distally. Paraglossa (Fig. 174) longer than ligula, hook shaped.

Thorax. Pronotum (Fig. 180) suboval in shape; posterior angle completely rounded; side with a prominent very flattened lateral depression sharply delimited from convex disc by discrete groove; lateral bead complete but fine; apical and basal beads present laterally, and in some specimens also medially; microsculpture of isodiametric mesh, but obsolescent medially in some specimens.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindfemur with 2 to several long setae on posterior margin. Hindtarsus with segment I shorter than II + III. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with apex of segment I in many specimens and all of segments II to IV in all specimens laterally expanded and spongy pubescent beneath.

Elytron. Intervals flat to slightly convex and with numerous small non-setigerous punctures; interval III with dorsal setigerous puncture about 1/4 way from apex; interval VII with very small ocellate puncture at extreme apex and large prominent ocellate puncture slightly more proximally located.

Abdomen. Sterna III to V with extra setae; sternum VI of ♂ with 2 pairs of ambulatory

setae; sternum VI of ♀ with distal margin enlarged medially to form prominent plate-like area in posterior view (Fig. 205).

Male genitalia. Median lobe with membranous area of dorsum relatively short, not reaching basal bulb, exact proximal boundaries not discernible; lacking apical disc.

Female genitalia. Valvifer (Fig. 232) moderately sclerotized and moderately convex, with several prominent distal setae; lateral dorsal margin connecting to membranous flap containing setae, flap joined to tergum. Stylus with basal segment bearing several setae on distal lateral and mesal margins. Spermatheca with distal annulated portion short and stout (Fig. 238).

Discussion. — This genus is well characterized by the prominent plate-like area on the distal margin of the female sixth abdominal sternum and the short, stout distal annulated portion of the spermatheca. The 3 currently recognized species together with their ranges are: *castelnaui* Csiki, 1932, Queensland, western Australia, and Tasmania; *interioris* (Castelnau), 1867, western Australia; and *opacipennis* (Chaudoir), 1878, south-western Australia. I have not obtained specimens of the latter species. Additional undescribed species may exist in Australia, and the species of the genus are in need of revision.

5 genus *Hypharpax* MacLeay

Hypharpax MacLeay, 1825: 22. [as subgenus of *Harpalus*]. [TYPE SPECIES: *Harpalus (Hypharpax) lateralis*, MacLeay, 1825, by monotypy, = *dentipes* (Wiedeman, 1823): 54].
Sagraemerus Redtenbacher, 1868: 13. [TYPE SPECIES: *Sagraemerus javanus* Redtenbacher, 1868: 14, by monotypy, = *dentipes* (Wiedemann, 1823): 54].

Description. — Body length approximately 7 to 13 mm.

Color. Body black to dark piceous.

Head. Labral apex slightly to strongly emarginate medially. Clypeal apex straight to moderately emarginate medially. Frons with frontal fovea punctiform, with or without clypeo-ocular prolongation. Gena wide, narrowest part between eye and mouth wider than maximum width of first antennal segment in most specimens. Mentum with very prominent median tooth in most specimens, tooth only moderately prominent in some specimens. Mentum separated from submentum by complete transverse suture. Ligula narrow, not expanded at apex. Paraglossa slightly longer than ligula, removed distally from it.

Thorax. Pronotum with posterior angle broadly rounded in most species, sharp or acute in few species; lateral bead complete; apical and basal beads present at least laterally.

Legs. Foretarsus with distal portion moderately expanded laterally; apical spur lanceolate. Hindfemur with various numbers of long setae on posterior margin. Hindtarsus with segments stout; segment I not to slightly more than twice as long as wide at apex and always shorter than II + III. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath or not laterally expanded and with small patch of spongy pubescence on venter of each segment.

Elytron. Intervals flat to convex; interval III with or without dorsal setigerous puncture; interval VII in most species with small ocellate puncture at extreme apex and large prominent ocellate puncture slightly more proximally located.

Hind wing. Full and apparently functional.

Abdomen. Sterna with varied number of setae.

Male genitalia. Median lobe lacking apical disc.

Female genitalia. Valvifer vestigial and very weakly sclerotized in most species. Stylus weakly sclerotized and with apical segment lobe like in most species. Proctiger absent or ves-

tigial in some species.

Discussion. — *Sagraemerus* was based on a species now known to be conspecific with the type species of *Hypharpax*. The genus *Hypharpax* is distributed from Tasmania, through Australia to New Guinea, Sumatra, Java, and the Celebes, and is also found in New Zealand. Most of the 30 known species are recorded from Australia. The species are: *abstrusus* Bates, 1878; *aeris* (Dejean), 1829 ♀*; *antarcticus* (Castelnau), 1867; *australis* (Dejean), 1829 ♂*; *bostocki* (Castelnau), 1867 *; *celebensis* Chaudoir, 1878 ♀*; *dampieri* (Castelnau), 1867 (one badly damaged female seen, has segment I of hindtarsus = to II + III and probably belongs in subgenus *Anisotarsus*, additional material needs to be examined); *dentipes* (Wiedemann), 1823; *deyrollei* (Castelnau), 1867 ♀*; *flavitarsis* Chaudoir, 1878 *; *flindersi* (Castelnau), 1867 ♂*; *habitans* Sloane, 1898 *; *inornatus* (Germar), 1848 *; *interioris* Sloane, 1895 *; *kingi* (Castelnau), 1895 *; *krefti* (Castelnau), 1867; *moestus* (Dejean), 1829 ♂*; *nitens* Sloane, 1910 *; *obsoletus* Blackburn, 1892; *opacipennis* MacLeay, 1888 *; *peroni* (Castelnau), 1867; *puncticollis* MacLeay, 1888 *; *queenslandicus* (Csiki) 1932; *ranula* (Castelnau), 1867; *rotundipennis* Chaudoir, 1878; *sculpturalis* (Castelnau), 1867 ♂*; *simplicipes* Chaudoir, 1878 *; *sloanei* Blackburn, 1891 ♀*; *varus* MacLeay, 1888 *; and *vilis* Blackburn, 1891. The species *antarcticus*, *flindersi* and *queenslandicus* listed as *Diaphoromerus* by Csiki (1932) actually belong in *Hypharpax* since they have stout, short hindtarsi, vestigial valvifer and stylus with lobe-like apical segment. The species of *Hypharpax* are not well understood and need revision.

6 genus *Gnathaphanus* MacLeay

Gnathaphanus MacLeay, 1825: 20. [TYPE SPECIES: *Gnathaphanus vulneripennis* MacLeay, 1825, by monotypy.].

Pachauchenius MacLeay, 1864: 116. [TYPE SPECIES: *Pachauchenius laeviceps* MacLeay, 1864, by monotypy, = *philippensis* (Chevrolat), 1841].

Mirosarus Bates, 1878b: 319. [TYPE SPECIES: *Mirosarus insularis* Bates, 1878, by monotypy, = *meliourensis* (Castelnau), 1867].

Description. — Body length approximately 7 to 17 mm. Body slender to moderately stout.

Color. Various.

Head. Head often relatively large. Labral apex straight to slightly emarginate medially. Clypeal apex straight to moderately emarginate medially. Frons with fovea punctiform. Mentum with prominent tooth in most species. Mentum and submentum separated by complete transverse suture. Ligula narrow, not expanded at apex. Paraglossa slightly longer than ligula.

Thorax. Pronotum with posterior angle moderately to broadly rounded in most species; lateral bead complete; apical and basal beads present at least laterally.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate, angulate medially on each side, or swollen basally. Hindfemur in most specimens with 2 long setae on posterior margin. Hindtarsus with segments slender and elongate; first segment 3 to 6 times as long as wide at apex and longer than II + III. Fore- and midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals flat to strongly convex; number of setigerous dorsal punctures and intervals on which such punctures located varied according to species, always however with at least 3 dorsal setigerous punctures on apical 1/3 to 1/4 of interval III; interval VII with small ocellate puncture at extreme apex and large prominent ocellate puncture slightly more proximally located.

Hind wing. Usually full and apparently functional.

Abdomen. Sternum VI with 1 or 2 pairs of ambulatory setae in ♂.

Male genitalia. Median lobe lacking apical disc.

Female genitalia. Valvifer moderately sclerotized, and in most species with few distal setae; shape various but distal lateral margin at least slightly emarginate in most species.

Discussion. — The species of this genus are concentrated in Australia; several also are present in Malasia and adjacent Asia; a few widely distributed species reach India, the Philippines and islands east to Samoa and New Caledonia; 2 species are recorded from China and 1 from the Ryukyu Islands of Japan. In addition, Habu (1973) has tentatively transferred *Iwosiopelus masaudai* Nakane and Ishida, 1959, found on the island of Iwo Jima, Japan, to the genus *Gnathaphanus*. I have not examined the single known specimen (a female) of this species, and Habu's transfer was only tentative. Therefore I have not included this species in the list of those belonging to *Gnathaphanus*. Darlington (1968) mentioned: "Of the 5 species known in New Guinea, all are shared with Australia and several are widespread also on the Malay Archipelago or islands of the western Pacific. These insects are often common in open country including grassland and open woodland, but are not often found in rain forest. All species of the genus that I know are fully winged and probably fly." The 25 currently recognized species are: *aridus* Blackburn, 1892*; *chinensis* Schaubberger, 1932*; *chujoii* Habu, 1973*; *denisonensis* (Castelnau), 1867*; *froggatti* (MacLeay), 1888*; *glamorgani* (Lequillon), 1841*; *goryi* (Gory), 1833*; *kansuensis* Schaubberger, 1932*; *herbaceus* Sloane, 1899*; *latus* Sloane, 1899*; *licinoides* Hope, 1842; *melbournensis* (Castelnau), 1867; *minutus* (Castelnau), 1867*; *parallelus* Louwerens, 1962*; *papuensis* (MacLeay), 1876*; *philippensis* (Chevrolet), 1841; *picipes* (MacLeay), 1864; *pulcher* (Dejean), 1829; *punctifer* (Castelnau), 1867*; *rectangulus* Chadoir, 1878*; *riverinae* Sloane, 1894; *sculpturalis* (Castelnau), 1867*; *subolivaceus* (MacLeay) 1825; *upolensis* (Csiki), 1915; *vulneripennis* MacLeay, 1825; *whitei* Sloane, 1907. The species *glamorgani*, *goryi*, *minutus*, *papuensis*, and *sculpturalis* were listed as tentative members of the genus by Csiki (1932). The species of *Gnathaphanus* are poorly understood, and in need of revision.

Pachauchenius and *Microsarus* were monotypic genera each based on a form now regarded as conspecific with a species of *Gnathaphanus*.

7 genus *Pseudanisotarsus* NEW GENUS

(Figs. 182, 239)

TYPE SPECIES: *Anisotarsus nicki* van Emden, 1953 here designated.

Description. — Body length 9.54 to 10.8 mm. Body form similar to that of subgenus *Anisotarsus*.

Head. Frons with fovea punctiform, obsolescent. Mentum lacking tooth. Mentum and submentum separated by complete transverse suture. Ligula narrow, not expanded at apex; with 4 to 5 distal dorsal setae. Paraglossa slightly longer than ligula.

Thorax. Pronotum (Fig. 182) with irregular series of setigerous punctures along lateral margin and along lateral portions of basal and apical margins.

Elytron. Intervals I, III, V, and VII each with row of setigerous punctures extended from base to apex and in most specimens situated along next odd stria; interval VII with small setigerous sub-ocellate puncture near apex and slightly more proximal ocellate puncture; intervals IX and X and apex of all intervals with numerous setigerous punctures.

Hind wing. Full and apparently functional.

Abdomen. Sterna with numerous extra setae of varied length; sterna III to V each with 1 pair of ambulatory setae; sternum VI of ♂ with 2 pairs of ambulatory setae.

Male genitalia. Median lobe with membranous area of dorsum reaching basal bulb; lacking apical disc but with apex prominently arrow shaped; apex concave just distal to end of dorsal membranous area. Everted internal sac with varied field of scales and spine-like scales.

Female genitalia. Valvifer (Fig. 239) reduced to small, weakly sclerotized transverse plate; apical portion membranous and without discrete boundaries. Stylus (Fig. 239) dorso-ventrally flattened, lobe like; apical and basal segments fused, separated by only faint groove; apical segment in many specimens with 1 to 2 short proximal setae. Proctiger absent.

Discussion. — This genus contains only *nicki*, originally described as a subspecies of *Notiobia (Anisotarsus) tucumana* by van Emden (1953) though it is clearly a separate species and also differs greatly from all members of *Notiobia (sensu lato)*. The shape and symmetry of the median lobe as opposed to the asymmetric median lobe of *tucumana* is itself sufficient to warrant separate specific status for *nicki*. The peculiar punctuation of the elytron, setigerous punctures of the pronotum, and vestigial transverse valvifer, distinguish *nicki* from all species of *Notiobia (sensu lato)*. In addition, the combination of 4 to 5 distal dorsal setae of the ligula, stylus with fused segments, and complete absence of proctiger distinguish *nicki* from all other species of the subtribe. Each of the last 3 characters is in itself sufficient reason to place *nicki* in a separate genus.

Since the species *nicki* has not been fully described, I am providing a description in this paper.

Pseudanisotarsus nicki NEW COMBINATION AND NEW STATUS

Anisotarsus tucumanus nicki van Emden, 1953: 520. [Probable paratype examined at BMNH (see discussion)].

Description.

Color. Dorsum with labrum dark piceous, lateral and apical margins of many specimens rufotestaceous to rufopiceous; remainder of head, pronotum, and elytron blue, bluish green, or green; relative darkness of head, pronotum, and elytron often varied in individual specimens. Venter rufopiceous to piceous, lateral portions often with violaceous, bluish, bluish-green, or green tinge.

Head. Labral apex strongly emarginate medially. Clypeal apex slightly emarginate medially. Supra-antennal ridges strongly convergent anteriorly. Frons with microsculpture of isodiametric mesh.

Thorax. Pronotum (Fig. 182) with side evenly curved towards posterior angle; posterior angle rounded; lateral depression obsolete; lateral bead complete; apical bead present laterally; basal bead complete or interrupted medially; basal fovea obsolescent; microsculpture of isodiametric mesh. Prosternum densely pubescent with moderately long setae.

Legs. Foretibia with apical spur lanceolate. Hindfemur with 8 to 20 long setae on posterior margin. Hindtarsus with segment I shorter than II + III. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Humerus rounded; subapical sinuation obsolescent; sutural angle broadly rounded; microsculpture of isodiametric mesh.

Variation. — I have not seen enough specimens to evaluate whether the observed variation is intra- or interpopulational.

Discussion. — The BMNH contains 1 male and 1 female of *nicki*. The male is labeled: "Type", "Argentina Prov. Buenos Aires 12.38. F. Shade", "Gesch. 3. 1939 von F. Schade", "nicki Emd type", "F. van Emden Bequest B. M. 1960-129". As van Emden stated "Bahia Blanca, Prov. Buenos Aires, xi. 46, ♂ type, 1 ♀ paratype (Ni.), 1 ♀ paratype (Emd.); Prov. Buenos Aires, xii. 38 (F. Schade), 1 ♂ paratype (Emd.)," the male bearing a type label at the BMNH is a paratype and not a holotype. From introductory information given by van

Emden "(Ni)" refers to "Dr. G. H. Nick, Sao Paulo (private collection)"; probably the holotype is in Brazil. The female specimen is labeled as being a paratype and as being collected at San Paulo, Brazil, but van Emden (1953) mentioned no specimens from Brazil.

The type labels on both the male and female specimens appear to be those used by van Emden (B. Brown, pers. commun.). Therefore, van Emden may have considered the male to be a holotype. I have noticed possible labeling errors in specimens of other species handled by van Emden so the exact status of the specimens at the BMNH can not be determined here.

Fortunately there is no confusion over the proper identification of *nicki* since van Emden illustrated its median lobe and described its pronotal, elytral and abdominal pubescence.

Distribution. — This species has been taken from areas in the Buenos Aires Province of Argentina. The female in the BMNH with the San Paulo label may be from San Paulo or possibly it may have been borrowed from a private collection housed at San Paulo and subsequently mislabeled.

Material examined (10 specimens)

ARGENTINA

PROVINCE BUENOS AIRES: Bahia Blanca, 2 ♂♂, 6 ♀♀, Hayward-Willimk (seen in private collection of J. Négre, Versailles, France); no specified locality, 1 ♂, at BMNH labeled as described above.

BRAZIL

PROVINCE SAN PAULO: San Paulo, 1 ♀, (BMNH) (perhaps mislabeled as explained above).

8 genus *Criniventer* van Emden

Criniventer van Emden, 1953: 519. [TYPE SPECIES: *Anisodactylus rufus* Brulle, 1838, by monotypy and original designation].

Description. — Body length approximately 9 mm. Body form as in subgenus *Anisotarsus*.

Color. Body rufous to light rufopiceous. Legs and palpi testaceous.

Head. Frons with fovea obsolescent but with clypeo-ocular prolongation; microsculpture of isodiametric mesh. Mentum with prominent tooth. Mentum and submentum separated by complete transverse suture. Ligula strongly expanded laterally at apex. Paraglossa slightly longer than ligula.

Thorax. Pronotum strongly cordate; lateral depression broadly concave and sharply delimited from disc; lateral part of apex with setigerous punctures; base and apex with prominent non-setigerous punctures.

Legs. All femora pubescent. Hindtarsus with segment I shorter than II + III. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments not laterally expanded but with sparse spongy pubescence on venter of apex of segment I and all of II and III.

Elytron. Scutellar stria vestigial to absent; odd and in some specimens also even intervals with irregular row of fine, short setae; subapical sinuation absent.

Abdomen. Sterna with irregular short pubescence; sternum VI of ♂ with 1 pair of ambulatory setae.

Male genitalia. Median lobe with membranous area of dorsum extended to basal bulb; lacking apical disc.

Discussion. — This genus contains only the species *rufus* which is reported by van Emden

(1953) as occurring in Argentina, Chile and Uruguay. I have seen 3 males but not females.

9-11 genus *Notiobia* Perty

Notiobia Perty, 1830: 13. [TYPE SPECIES: *Notiobia nebrioides* Perty, 1830, by monotypy].

Description. — Body length 6.3 to 14.1 mm. Body form slender to moderately stout.

Head. Labral apex straight to prominently emarginate medially. Clypeus with apex straight, sinuate, or broadly emarginate medially, base of labrum exposed in many specimens with broadly emarginate apex. Frons with isodiametric microsculpture, obsolescent medially in some specimens. Mentum with prominent median tooth except in members of *tucumana* lineage. Mentum and submentum separated by complete transverse suture. Paraglossa slightly longer than ligula.

Thorax. Pronotum varied in shape; lateral depression absent to prominent; lateral bead complete but varied in prominence; apical and basal beads present at least laterally; basal and outer fovea various; microsculpture of isodiametric mesh, slightly stretched transversely or obsolete medially in some specimens. Pubescence of venter various.

Legs. Foretibia with apical spur lanceolate, slightly curved in some specimens. Hindfemur with 2 to 12 long setae on posterior margin. Hindtarsus with segment I shorter than II + III.

Elytron. Scutellar stria elongate in *umbrata* and *umbrifera*; microsculpture of isodiametric mesh in most specimens.

Hind wing. Full and apparently functional in most species, vestigial in *hilariola*, dimorphic in *cyanippa*.

Abdomen. Sterna with extra setae in species of the *tucumana* lineage of subgenus *Anisotarsus*; sternum VI of ♂ with 1 or 2 pairs of ambulatory setae. Apex of tergum VIII of ♀ various.

Male genitalia. Median lobe symmetrical except in *tucumana*; membranous area of dorsum extended to basal bulb except in *leiroides* and *parilis*; without apical disc in *Anisotarsus* and *Notiobia*, with apical disc in *Diatyphus*.

Female genitalia. Valvifer flat to slightly convex; lateral margin semi-membranous and without distinct boundary; apex with or without several setae (Fig. 129). Stylus varied in shape.

Discussion. — Previous authors have simply assumed *Notiobia* (s. str.) and *Anisotarsus* to be distinct genera. The only paper providing any information on possible differences between the two groups is that of van Emden (1953) who provided a key to the genera of Neotropical Anisodactylina. The characters utilized by him in the key to separate the two groups can be tabulated as follows:

Notiobia

Frontal impression large and deep, usually with clypeo-ocular prolongation which reaches eye. If clypeo-ocular prolongation absent, then supra-antennal ridges conspicuously divergent from middle of eyes to antennal insertion. Frons and vertex not very convex. Eye large and very convex. Pronotum always cordate, though often with obtuse posterior angle.

Anisotarsus

Frontal impression small and shallow. Supra-antennal ridges varied, if divergent from middle of eyes to antennal insertion, then gena wider than first antennal segment. Frons and vertex strongly and evenly convex. Eye rather small, moderately convex and not much protruding. Prothorax more often with side arcuate to posterior angle.

The above characters do not seem stable enough to warrant generic separation of *Notiobia* (s. str.) and *Anisotarsus* on phenetic grounds. In *Anisotarsus* the frontal fovea is always small, shallow and without a clypeo-ocular prolongation. While the frontal fovea in *Notiobia* (s. str.) is usually deep and large and with a clypeo-ocular prolongation, it does vary considerably. For example: *parilis* has a large, deep frontal fovea lacking a readily visible clypeo-ocular prolongation; *leiroides* has a moderately wide deep fovea lacking a clypeo-ocular prolongation; *obscura* has a relatively smaller and shallower fovea bearing a faint, short clypeo-ocular prolongation which does not reach the eye; *limbipennis* has a relatively large deep fovea bearing a prominent clypeo-ocular prolongation which reaches the eye; *disparilis* has a relatively large, deep frontal fovea which usually lacks any indication of a clypeo-ocular prolongation; *umbrifera*, *umbrata*, *melaena*, *wilkensi*, and *cooperi* have moderately wide deep fovea each bearing a clypeo-ocular prolongation which reaches the eye; *incerta* and *chiriquensis* have relatively small, shallow fovea each bearing a prominent clypeo-ocular prolongation which reaches the eye; and *cupreola* has a moderately wide fovea bearing a clypeo-prolongation of varying prominence and length.

The degree of divergence of the supra-antennal ridges also varies in *Notiobia* (s. str.). This variation does not appear to be correlated with the condition of the frontal fovea except that species completely lacking a clypeo-ocular prolongation have the supra-antennal ridges strongly divergent anteriorly. Within the *Anisotarsus* group, the species *cyanippa* and *brevicollis* have strongly divergent supra-antennal ridges while in *praeclarus* the ridges vary from slightly to strongly divergent, and in *cupripennis* they are moderately divergent. The remaining species within the *Anisotarsus* group have the supra-antennal ridges not or only slightly divergent.

I have not been able to recognize the difference in convexity of the frons and vertex which van Emden described.

The pronotum in *Notiobia* (s. str.) is strongly cordate in many species such as *parilis*, *disparilis* and *limbipennis*, but it is more evenly rounded from apex to base in other species such as *chiriquensis* and *ewarti*.

The eye of species of *Notiobia* (s. str.) and of the *Anisotarsus* group varies in relative size, convexity, and protrusion from the side of the head. In general, species of *Notiobia* have a relatively larger and more protruding eye, but there are many exceptions to this rule.

In addition to distinguishing characters given by van Emden the base of the pronotum is lobed in most species of *Notiobia* (s. str.) and non-lobed in most species of *Anisotarsus*.

In my opinion, these characters are not sufficient to separate the two groups as genera. I believe, however, that they are sufficient to warrant separate subgeneric status for each, and I here treat *Anisotarsus* as a subgenus of *Notiobia*.

Diatypus has until now been treated as a separate genus. However, I believe it has evolved from the same ancestor as has the subgenus *Notiobia*. I do not think species of *Diatypus* are phenetically different enough from those of *Notiobia* and *Anisotarsus* to warrant separate generic status. Species of *Diatypus* possess the same form of valvifer as found in species of *Notiobia* and *Anisotarsus*. And species of *Diatypus* agree with all species of *Notiobia* and most species of *Anisotarsus* in having a median mental tooth. In addition, the species of *Diatypus* (except for a few members of the "Paradiatypus" species group which have secondarily reverted to the plesiomorphic condition of small eye and wide gena) and those of *Notiobia* share the clearly apomorphic feature of narrow gena and large protruding eye. The only constant differences between species of *Diatypus* and of *Notiobia* and *Anisotarsus* are the possession by *Diatypus* species of extra dorsal setigerous punctures on the third elytral interval and an apical disc on the median lobe of males. These phenetic differences do not warrant separate generic status for *Diatypus*. However they do seem sufficient for subgen-

eric status. Therefore I am here proposing to treat *Diatypus* as a subgenus of *Notiobia*.

9 subgenus *Anisotarsus* Chaudoir NEW STATUS

Anisotarsus Chaudoir, 1837: 41. [TYPE SPECIES: *Anisotarsus brevicollis* Chaudoir, 1837, designated by van Emden, 1953: 519].

Diaphoromerus Chaudoir, 1843 a: 402. [TYPE SPECIES: *Diaphoromerus iridipennis* Chaudoir, 1843: 405, by monotypy. NEW SYNONYMY].

Eurytrichus LeConte, 1848: 287 [page incorrectly numbered "387" in paper]. [TYPE SPECIES: *Feronia terminata* Say, 1823, designated by van Emden, 1953: 525].

Stilboldius Casey, 1914: 171, 206. [TYPE SPECIES: *Harpalus mexicanus* Dejean, 1829, by original designation of Casey, p. 206-207].

Description. — Body length 5.3 to 14.1 mm.

Color. Various except antenna with distal 8 to 9 segments of most specimens each with longitudinal median dark bar.

Head. Frontal fovea small to obsolete and lacking clypeo-ocular prolongation. Eye small to large and protruding. Width of narrowest part of gena relative to maximum width of first antennal segment various; supra-antennal ridges varied from not divergent to strongly divergent anteriorly.

Thorax. Pronotum semi-rectangular; not strongly narrowed at base in most species. Venter, except for apex of prosternal lobe, glabrous unless otherwise noted.

Legs. Unless otherwise stated, ♂ fore- and midtarsi with apex of segment I and all of segments II - IV laterally expanded and spongy pubescent beneath. Hindfemur with 2 to 4 long setae on posterior margin in most species, 4 to 12 in members of *tucumana* lineage. Hindtarsus with segments slender and elongate; first segment 3 to 4 times as long as wide at apex and slightly shorter to slightly longer than II + III.

Elytron. Interval III, with 1 or 2 dorsal setigerous punctures; interval VII, unless otherwise stated, with small subocellate puncture (may be difficult to see) near apex and slightly more proximal larger ocellate punctures; microsculpture of isodiametric mesh unless otherwise stated.

Hind wing. Full and apparently functional in most species, vestigial in *hilariola*, dimorphic in *cyanippa*.

Abdomen. Sternum VI of ♂, unless otherwise noted, with 1 pair of ambulatory setae.

Discussion. — Blatchley (1910) in his pioneering work on the beetles of Indiana treated the 3 species found there as members of the genus *Anisodactylus*. Casey (1914) split *Anisotarsus* into 2 separate genera and then in 1924 proposed many new species which are today regarded as conspecific with previously described ones. Van Emden (1953) revised all the species and regarded *Anisotarsus* as a valid separate genus. However, he was mainly interested in the Neotropical fauna, he apparently had available only small series of most species, and he did not examine types deposited in North America. Consequently he failed to see crucial intergrades between various forms and was not able to properly assign synonyms to those species he recognized as valid. These errors are especially prominent in his treatment of the North American species. Lindroth (1968) in his fine work on the Carabidae of Canada and Alaska revised the 3 species found in Canada and also keyed out 3 others not occurring there. However, since he was primarily interested in northern forms, a complete revision of all the North American species together with an examination of the relationship of *Anisotarsus* to other supra-specific taxa is warranted. As discussed for the genus *Notiobia*, I feel that *Anisotarsus* is merely a subgroup of that genus. *Anisostichus* proposed by van Emden (1953) as a new subgenus of *Anisotarsus* is in my opinion a valid separate genus as discussed

under that taxon.

Diaphoromerus has until now been treated as a separate genus composed of species found in the Australian Region. However, E. Zimmerman while working on the Coleoptera of the Hawaiian Islands found several introduced species of *Diaphoromerus* there and therefore investigated the genus *Diaphoromerus*. He concluded that the species of *Diaphoromerus* are not sufficiently different in morphological characters from those of *Anisotarsus* (*s. str.*) to warrant separate generic status (pers. commun. to G. E. Ball). I agree with this conclusion since the only appreciable morphological differences between species of *Diaphoromerus* and *Anisotarsus* (*s. str.*) are: in members of *Anisotarsus* (*s. str.*) the dorsal membranous area of the median lobe is elongate and reaches the basal bulb and also segment I of the hindtarsus of most specimens is usually shorter than II + III; in members of *Diaphoromerus*, the length of the dorsal membranous area of the median lobe and the relative lengths of the first 3 segments of the hindtarsus vary. These differences certainly are neither constant nor fundamental. Therefore, I treat *Diaphoromerus* as congeneric with the subgenus *Anisotarsus*.

For convenience of workers studying the fauna of the New World and Australian Region the species of *Anisotarsus* may be grouped respectively into the "Anisotarsus" and "Diaphoromerus" species groups. The North American species of the "Anisotarsus" species group are revised in this paper. The remaining named forms of this group are found in temperate areas of South America and are: *bradytoides* (H. W. Bates), 1891; *tucumana* (Dejean), 1831; *peruviana* (Dejean), 1829; *elata* (Erichson), 1847; *margaretae* (van Emden), 1953; *stubeli* (van Emden), 1953; *praeclarus* (Putzeys), 1878; *cupripennis* (Germar), 1824; *latiusculus* (van Emden), 1953; *schnusei* (van Emden), 1953; *chalcites* (Germar), 1824; *amethystina* (Dejean), 1829. I have seen only males of *amethystina* but have examined both males and females of all the other named forms of South American *Anisotarsus*.

The "Diaphoromerus" species group is centered in Australia but has species also on New Zealand, New Guinea, New Caledonia, the Moluccas, and Timor; several of its species have also been introduced into the Hawaiian Islands. The 31 named forms of this group are: *angustula* (Chaudoir), 1878; *australasiae* (Dejean), 1829; *basilewski* (Louwerens), 1962 ♂*; *edwardsi* (Castelnau), 1867 ♀*; *flavipalpis* (MacLeay), 1864 ♀*; *germari* (Castelnau), 1867; *inaequalipennis* (Castelnau), 1867; *iridipennis* (Chaudoir), 1843; *lapeyrousei* (Castelnau), 1867; *laticollis* (MacLeay), 1888*; *ludicollis* (Dejean), 1829; *melanara* (Dejean), 1829; *nigrans* (MacLeay), 1888*; *oblongiuscula* (Castelnau), 1867*; *opaca* (MacLeay), 1888; *ovata* (Chaudoir), 1878*; *papuella* (Darlington), 1968; *papuensis* (Darlington), 1968; *patrueloides* (Castelnau), 1867; *perater* (Sloane), 1920*; *planiuscula* (Chaudoir), 1878*; *planoimpressa* (Castelnau), 1867 ♀*; *polita* (MacLeay), 1888*; *porcatula* (MacLeay), 1888*; *quadricollis* (Chaudoir), 1878*; *queenslandica* (Csiki), 1932; *rectangula* (Chaudoir), 1878; *rugosipennis* (Castelnau), 1867*; *sculptipennis* (Castelnau), 1867*; *sericipennis* (MacLeay), 1888*; *viridipennis* (Sloane), 1920*. The species *basilewski* is here transferred from the genus *Gnathaphanus* to the *Diaphoromerus* group of the subgenus *Anisotarsus*.

Members of the "Diaphoromerus" species group and the South American forms of the "Anisotarsus" species group are poorly understood and need revision.

Key to the North American Species of the Subgenus *Anisotarsus*

Notes concerning the key.

This section discusses the more difficult to understand characters used in the key. The user of this key will soon note that many species key out in more than one couplet. Each of the species of *Anisotarsus* is highly variable, and usually it is not possible to distinguish a given species on the basis of one or two constant characters as in *Notobia* and *Gynandrotarsus*. Rather, most species of *Anisotarsus* must be separated by a complex of characters

any one of which may be absent or highly modified on individual specimens.

The width of the narrowest part of the gena between the raised bead along the ventral edge of the eye and the mouth cavity relative to the maximum width of the first antennal segment is used in the first couplet. Species in which these widths are not closely correlated are treated in both halves of the couplet.

Body color is used extensively in the key. The color of a particular part of the body is generally easy to determine for a given specimen. However, in some species various body regions may exhibit faint to prominent metallic reflections or tinges in addition to their basic color. Illumination produced by an incandescent lamp is suitable for examination of these tinges, except for specimens keying to couplet 2 for which daylight or equivalent fluorescent light should be used. The perception of some tinges is affected by the angle at which light strikes the specimen; therefore a specimen being examined for a given tinge should be held under the microscope at several different angles. Particular care must be exercised when the specimen is teneral as characteristic tinges may be faint or even absent. Also, a specimen being examined for a tinge should first be cleaned by soaking it in hot detergent solution in order to remove grease and dirt, then rinsed to remove the detergent.

Body size has been used in several couplets and in each instance has been measured as described in the "Measurements" section.

The shape and structure of the median lobe are employed to separate species in several couplets. In some of these couplets mention is made of a prominent internal sac spine being visible beneath the membranous surface of the dorsum or in a few instances also projecting out into the ostium. In order to observe this spine, it is usually necessary to completely wet the median lobe by immersing it in boiling water. In some cases it may also be necessary to soak the median lobe in hot potassium hydroxide for approximately 1 minute in order to darken the spine and make the membranous area of the dorsum more transparent.

In order to construct a key which is not excessively long and which will separate all specimens encountered, I give geographical distribution in couplets 15, 16, 18 and 23. In these 4 couplets the ranges of the species being compared are either far removed from one another or else are used only as subsidiary aids after morphological characters separating the species have been provided.

Problems may be encountered in separating some specimens of *terminata* from *purpurascens*. Specimens of *terminata* which have a prominent lateral depression on the pronotum are easily separated in the key from *purpurascens* since the latter species never has this character.

Most specimens of *terminata* have a conspicuous greenish, aeneous, or cupreous tinge on the elytra while specimens of *purpurascens* completely lack such tinges or in a very few specimens have a faint greenish blue tinge. However, occasional specimens of *terminata* from southeastern United States, Mexico and Central America lack these tinges on the elytra and have at most a slight lateral depression on the pronotum. These specimens key to couplet 18. To reliably identify specimens keying to this couplet all sections of each half of the couplet should be read and compared.

Key to the North American Species of the Subgenus *Anisotarsus*

1	Narrowest part of gena at least as wide as maximum width of first antennal segment	2
-	Narrowest part of gena not as wide as maximum width of first antennal segment	6
2 (1)	Elytron with brassy, greenish, aeneous, or cupreous tinge or coloration	3
-	Elytron without indication of such tinges or coloration	4
3 (2)	Posterior angle of pronotum rounded (Fig. 8); median lobe (Figs. 89, 90)	

with moderately long tapering apex, prominent spine visible beneath membrane of dorsum near ostium and projected into ostium (in part) *hilariola* (H. W. Bates), p. 302

— Posterior angle of pronotum not rounded (Fig. 1); median lobe (Figs. 77, 78) with shorter, blunter apex, lacking prominent spine *lamprota* (H. W. Bates), p. 318

4 (3) Pronotum with posterior angle subdente (only on one side in some specimens), projected latero-posteriorly and lateral bead thick especially posteriorly (Fig. 5); median lobe without large internal spine *mexicana* (Dejean), p. 320

— Pronotum with posterior angle obtusely rounded to nearly acute, not subdente and lateral bead not thick (Figs. 6, 14); median lobe with prominent spine visible in membranous area of dorsum 5

5 (4, 19) Pronotum with posterior angle rounded (Fig. 6); apex of abdominal sternum VI with 1 pair of ambulatory setae in ♂; hind wing vestigial in most specimens, full in some specimens (in part) *cyanippa* (H. W. Bates), p. 302

— Pronotum with posterior angle right or slightly obtuse (Fig. 14); apex of abdominal sternum VI with 2 pairs of ambulatory setae in ♂; hind wing full *brevicollis* (Chaudoir), p. 300

6 (1) Elytron with conspicuous greenish, brassy, or aeneous tinge 7

— Elytron lacking conspicuous greenish, brassy, or aeneous tinge 11

7 (6) First segment of antenna with central portion black or piceous, apices lighter in some specimens; dorsum of hind tarsus black or piceous; median lobe as in Figs. 89, 90 (in part) *hilariola* (H. W. Bates), p. 302

— First segment of antenna testaceous, rufotestaceous, or rufous; dorsum of hind tarsus same color as first segment of antenna, except darker in some specimens of *virescens* 8

8 (7) Head with eye reduced and not strongly protruding (Fig. 39) (in part) *nitidipennis* (LeConte), p. 305

— Head with eye large and strongly protruding (Fig. 38) 9

9 (8) Pronotum with prominent lateral depression originating near anterior angle and rapidly widened posteriorly, side broadly flattened in region of posterior angle (Figs. 10, 11); dorsum of hind tarsus testaceous or rufotestaceous (in part) *terminata* (Say), p. 313

— Pronotum with lateral depression absent or if present prominent only in region of lateral seta, side not broadly flattened in region of posterior angle (Figs. 2, 12, 13) 10

10 (9) Median lobe with apex sharply pointed in dorsal view (Figs. 61, 63, 65); dorsum of hind tarsus testaceous to rufotestaceous; microsculpture of pronotum of normal isodiametric mesh; range United States to Panama (in part) *terminata* (Say), p. 313

— Median lobe with apex bluntly rounded in dorsal view (Fig. 69); dorsum of hind tarsus testaceous, rufotestaceous, rufopiceous, piceous, or black; microsculpture of pronotum consisting of extremely prominent isodiametric mesh; range central Mexico (in part) *virescens* (Dejean), p. 308

11 (6) Body brown to piceous brown, or rarely piceous, without metallic tinges; AND microsculpture of pronotum obsolete medially; AND abdominal sternum VI with 2 pairs of ambulatory setae in both sexes *picea* (LeConte), p. 309

— Combination of characters not as above 12

12 (11) Pronotum with prominent lateral depression rapidly widened posteriorly, side broadly flattened in region of posterior angle (Figs. 9, 10) 13

— Pronotum with lateral depression absent or if present prominent only near lat-

eral seta, side not broadly flattened in region of posterior angle (Figs. 2, 3, 4, 6, 12, 16) 14

13 (12) Dorsum of hind tarsus black or piceous; median lobe with blunt apex in dorsal view (Fig. 83) (in part) *maculicornis* (Chaudoir), p. 307

— Dorsum of hind tarsi testaceous, rufotestaceous, or rufous; median lobe with tapered apex in dorsal view (Fig. 61) (in part) *terminata* (Say), p. 313

14 (12) Dorsum of hind tarsus testaceous or rufotestaceous 15

— Dorsum of hind tarsi piceous or black 19

15 (14) Head with eye reduced, not prominent (Fig. 39); posterior angle of pronotum projected in some specimens (Fig. 16); range Canada and eastern United States (in part) *nitidipennis* (LeConte), p. 305

— Head with eye large, prominent (Fig. 38); posterior angle of pronotum not projected; range southern United States and Mexico 16

16 (15) Median lobe with short blunt apex in dorsal view (Fig. 71); body brown to reddish brown; pronotum without outer fovea; first antennal segment testaceous to rufous; range Guadalupe Island, southern tip of Baja California, and Mazatlan region of western Mexico *flebilis* (LeConte), p. 310

— Median lobe with apex various; body color of most specimens not brown or reddish brown; pronotum with or without fovea; range California, Arizona, eastern United States, eastern and Central Mexico; OR if specimen from southern tip of Baja California then first antennal segment with central portion along posterior margin black or dark piceous, apices lighter in some specimens 17

17 (16) Median lobe with blunt apex in dorsal view (Fig. 69); head and pronotum in most specimens with prominent greenish or purplish tinge; microsculpture of head and pronotum of prominent, sub-granulate isodiametric mesh (in part) *virescens* (Dejean), p. 308

— Median lobe with apex tapered in dorsal view (Figs. 63, 65, 67); head and pronotum without prominent greenish or bluish tinge, with or without purplish or slight greenish tinge; microsculpture of head and pronotum of normal isodiametric mesh, not sub-granulate 18

18 (17) Elytron piceous to rufopiceous, in some specimens with slight cupreous tinge, not with purple coloration; AND specimen from southeastern United States (as far west as eastern Arizona), Mexico, or Central America; AND pronotal sides various posteriorly; AND median lobe more slender in dorsal view (Figs. 63, 65) (in part) *terminata* (Say), p. 313

— Elytron purplish, purplish-piceous, bluish or purplish black; AND specimen from California, Arizona, Gulf region of southeastern United States, or Mexico; AND pronotal sides strongly convergent posteriorly (Fig. 3); AND median lobe stouter in dorsal view (Fig. 67) *purpurascens* (H. W. Bates), p. 311

19 (14) First segment of antenna testaceous, rufotestaceous, or rarely rufopiceous 20

— First segment of antenna with central area black, dark piceous and in some specimens apices lighter; or first segment, infuscated along center of posterior edge 5

20 (19) Head with eye reduced and not strongly protruding (Fig. 39); specimen from Canada or United States (in part) *nitidipennis* (LeConte), p. 305

— Head with eye large and strongly protruding (Fig. 38); or if eye not large and

protruding specimen from central or southern Mexico 21

21 (20) Posterior angle of pronotum rounded (Figs. 2, 6); pronotum and elytron purplish black, bluish black or purple; side of pronotum not sinuate before posterior angle; hind wing vestigial or full 22

— Posterior angle of pronotum subdenteate or right (Figs. 4, 9) and side of pronotum of some specimens sinuate before posterior angle; pronotum and elytron black or piceous; hind wing full 23

22 (21) Median lobe with prominent spine projected from ostium (Fig. 87); hind wing of most specimens vestigial; pronotum with sides more strongly convergent posteriorly and posterior angle of most specimens more broadly rounded (Fig. 6); microsculpture of pronotum of normal isodiametric mesh, disc in many specimens shiny, especially in ♂
..... (in part) *cyanippa* (H. W. Bates), p. 302

— Median lobe without spine projected from ostium (Fig. 69); hind wing full; pronotum with sides less strongly convergent posteriorly and posterior angle of most specimens less broadly rounded (Fig. 2); microsculpture of pronotum of very prominent sub-granulate isodiametric mesh, disc not shiny (in part) *virescens* (Dejean), p. 308

23 (21) Abdominal sternum VI with 2 pair of ambulatory setae in ♂; body length 8.3 to 9.5 mm.; range central Mexico *schlingeri* new species, p.

— Abdominal sternum VI with 1 pair of ambulatory setae in ♂; body length 12.7 to 13.1 mm.; range southeastern United States
..... (in part) *maculicornis* (Chaudoir), p. 307

9.1 *Notiobia* (*Anisotarsus*) *brevicollis* (Chaudoir)
(Figs. 14, 85, 86, 139)

Anisotarsus brevicollis Chaudoir, 1837: 42. [Lectotype (MNHP), here designated, ♀ labeled: "Puebla.", "Ex Musaeo Chaudoir", "Bates vidit 1881". Label added stating: "LECTOTYPE Anisotarsus brevicollis Chaudoir By G.R. Noonan". TYPE LOCALITY: Mexico originally cited by Chaudoir, here restricted to state of Puebla, Mexico].

Anisotarsus laeviusculus Chaudoir, 1837: 43. [Lectotype (MNHP), here designated, ♂ labeled: "Ex Musaeo Chaudoir". Label added stating: "LECTOTYPE Anisotarsus laeviusculus Chaudoir By G.R. Noonan". TYPE LOCALITY: Mexico as originally cited.]

Description. — Body length 8.2 to 14.1 mm.

Color. Dorsum piceous to black, slightly shiny in some specimens; lateral margins of labrum and elytral epipleura somewhat lighter in many specimens. Venter, legs, and palpi rufopiceous to black. First segment of antenna with center black or piceous and in some specimens apices lighter, or rarely first segment with center of posterior margin infuscated to black and remainder lighter.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex slightly to moderately broadly emarginate medially. Frons as in *terminata*. Width of narrowest part of gena equal to or greater than maximum width of first antennal segment.

Thorax. Pronotum (Fig. 14) with posterior angle prominent, slightly obtuse to very slightly projected; lateral depression narrow, obsolescent to moderate; basal bead complete; microsculpture of isodiametric mesh. Prosternum glabrous medially, in some specimens with fine short scattered pubescence elsewhere. Mesosternum glabrous in most specimens, sparsely finely pubescent in others. Metasternum with scattered setae in region of midcoxa.

Legs. Dorsum of tarsi moderately to densely pubescent.

Elytron. Humerus angulate, in most specimens with small tooth; intervals flat; interval I in most specimens with 1 or more apical setigerous punctures; interval II with setigerous puncture about 1/3 forward from apex; subapical sinuation slight to moderate; sutural angle rounded.

Abdomen. Sternum VI with 2 pairs of ambulatory setae in ♂.

Male genitalia. Median lobe (Figs. 85, 86) relatively stout; apex short, bluntly rounded at tip, bent ventrad. Internal sac in repose with large prominent spine visible beneath membranous area of dorsum; everted sac with the large spine proximal to median lobe and with distal field of enlarged scales.

Variation. — Intrapopulational variation occurs in: body size and color; emargination of labral and clypeal apices; width of gena; prominence of pronotal posterior angle; prominence of pronotal lateral depression; pubescence of prosternum; and prominence of elytral subapical sinuation.

Discussion. — The description of *laeviusculus* immediately follows the description of *brevicollis*; Chaudoir noted the resemblance but stated *laeviusculus* to be more narrow and convex. Van Emden (1953) correctly treated *laeviusculus* as conspecific with *brevicollis*.

Flight. — Members of this species have not been taken at light or observed flying.

Bionomics. — Members of this species have been taken from January to November and at altitudes from 1,550 to 9,030 feet.

Within the United States this species appears to be restricted to forests predominantly of pine, oak, and possibly walnut, in mountainous areas of Arizona, New Mexico, and Texas. During the nights of September 4 and 5, 1969, I collected a total of 52 specimens at the Southwest Research Station, 5 mi. W. Portal, Arizona, which were found along a trail leading to a small creek. They did not seem however to be associated with the creek and were found no closer to it than approximately 5 yards. They were restricted to a portion of the trail shaded by pines and oaks during part of the day. The ground in the collecting area had scattered short grass and leaves on it and was bare in spots. The beetles were observed resting on the surface, crawling over the ground and mating. One female was seen eating the remains of a scarab head. No specimens were found along the trail during daylight hours.

Elbert Sleeper provided me with information on the vegetation in the La Laguna area of Baja California, and it is clear from his information that the species occurs there in the Lagunan Woodland as defined by Axelrod (1958).

Within mainland Mexico *brevicollis* occurs in a wide variety of habitats. Ball's data indicate it has been taken on the ground under debris or rocks in: forests of oak, pine, madrone and manzanita, and mixture of sycamore and walnut; along the edges of agricultural areas such as cornfields and sugar cane fields; along roadsides; in pastures and meadows; and by pools or streams in a variety of different habitats. It has also been taken: in cut-over tropical deciduous forest 9.5 mi. W. Morelia, 6,250 feet; in *Eucalyptus* woods in Mexico City; and under stones on open ground in an area with remains of cloud forest adjacent to intact cloud forest at Omiltemi, 7,300 feet. Specimens were taken by D.R. Whitehead in pinyon pine country 15.7 mi. W. Durango on January 11, when the ground was frosted. The beetles were aggregated under large rocks near pools adjacent to a stream.

Distribution and material examined (807 specimens). This species is centered in mainland Mexico but extends into mountainous areas of Arizona, New Mexico, Texas, and the Sierra Lagunas of southern Baja California (Fig. 139).

9.2 *Notiobia (Anisotarsus) cyanippa* (H. W. Bates)
(Figs. 6, 87, 88, 140)

Anisotarsus cyanippus H. W. Bates, 1882: 51. [Lectotype (BMNH), here designated, ♂ labeled: "Type H. T.", "Cuernavaca", "Mexico, Salle Coll.", "B.C.A. Col. I. 1. Anisotarsus cyanippus Bates ♂". Labels added stating: "Lectotype" and "LECTOTYPE Anisotarsus cyanippus Bates By G. R. Noonan". TYPE LOCALITY: Cuernavaca and Capulalpam, Mexico originally cited, here restricted to Cuernavaca, Morelos, Mexico].

Description. — Body length 10.1 to 13.3 mm.

Color. Dorsum black, bluish black, or purplish black, shiny in many specimens. Venter and legs rufopiceous to black. Palpi rufopiceous to piceous. Antenna with first segment infuscated to black along at least central posterior margin.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex straight to slightly broadly emarginate medially. Frons as in *terminata*. Gena as in *brevicollis*.

Thorax. Pronotum (Fig. 6) with posterior angle obtusely rounded; lateral depression shallow or obsolescent, especially posteriorly; lateral bead prominent; basal bead complete; basal and outer fovea various; microsculpture of isodiametric mesh. Venter as in *brevicollis*.

Legs. Dorsum of tarsi moderately to densely pubescent.

Elytron. Humerus somewhat angulate; microsculpture in ♂ of isodiametric mesh becoming granulate laterally, in ♀ of granulate isodiametric mesh; remainder as in *terminata*.

Male genitalia. Median lobe (Figs. 87, 88) with apex short, slightly removed to right in dorsal view. Internal sac in repose with prominent spine visible beneath dorsum in region of ostium, in some specimens this spine projected through ostium.

Flight. — Most specimens examined had vestigial wings, but 3 specimens had normal wings and were taken at black light 5.4 and 9.1 mi. E. Cuernavaca in June and July.

Bionomics. — Members of this species have been taken from June to November and at altitudes from 4,340 to 6,800 feet. Ball's data indicate *cyanippa* has been taken: at black light in thorn forest with old lava flow substrate 5.4 mi. E. Cuernavaca, 4,600 feet; under cover on damp ground consisting of old lava flow 3.6 mi. E. Cuernavaca, 4,600 feet; at black light on sides of steep canyon with subtropical deciduous, rather open vegetation 9.1 mi. E. Cuernavaca, 4,300 feet; in wet, deep litter on slopes of southwest-facing ravine with bromeliads in oak forest 26.1 mi. S. Tecalitlan, 6,800 feet; and under stones and in litter from few trees near small creek bed at the edge of corn field in vicinity of tropical montane forest 6.5 mi. S. Talpa de Allende, 4,340 feet.

9.3 *Notiobia (Anisotarsus) hilariola* (H. W. Bates)
(Figs. 8, 89, 90, 143)

Anisotarsus hilariolus H. W. Bates, 1891: 239. [Lectotype (BMNH), here designated, ♂ labeled: "Lectotype", "Omilteme Guerrero 8000 ft. July. H. H. Smith", "Anisotarsus hilariolus Bates". Label added stating: "LECTOTYPE Anisotarsus hilariolus Bates By G. R. Noonan". TYPE LOCALITY: Omilteme, Guerrero, 8,000 ft., Mexico as originally cited].

Description. — Body length 10.9 to 11.3 mm.

Color. Dorsum somewhat shiny, especially in ♂; labrum rufopiceous to black, remainder of head dark blue, dark purple, bluish black, or purplish black; pronotum dark blue, dark purple, or greenish purple, coloration more prominent than in head; elytron greenish or aeneous and in some specimens with cupreous tinge (coloration of dorsum best observed

under natural daylight or under equivalent light from fluorescent lamp). Venter and palpi piceous to rufopiceous. Legs rufopiceous, to black. Antenna with first 3 segments piceous to rufopiceous.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex slightly emarginate medially. Frons with microsculpture of isodiametric mesh, obsolescent medially in ♂. Width of gena and first antennal segment as in *lamprota*. Supra-antennal ridge arcuate, curved first outwards then inwards.

Thorax. Pronotum (Fig. 8) with posterior angle rounded; anterior angle prominent; lateral bead prominent, especially near posterior angle; basal bead complete; microsculpture of isodiametric mesh, obsolescent medially in ♂, not obsolescent medially in ♀ but less prominent medially than laterally. Prosternum with scattered fine short setae elsewhere except medially. Proepimeron with fine short pubescence near front coxae. Mesosternum with fine short pubescence in some specimens. Metasternum with irregular short fine pubescence in region of midcoxae.

Legs. Dorsum of tarsi pubescent.

Elytron. Humerus of some specimens with faint indication of tooth; intervals flat to slightly convex; interval III with setigerous puncture at apical 1/3 or 1/4; subapical sinuation slight to moderate; sutural angle rounded; microsculpture in ♂ of isodiametric mesh and nearly obsolete medially, in ♀ of isodiametric mesh and slightly less prominent medially.

Abdomen. One ♂ from Omiltemi, Guerrero with 2 pairs of ambulatory setae on sternum VI.

Male genitalia. Median lobe (Figs. 89, 90) with apex relatively elongate; sclerotized virga present to left of ostium; large prominent spine, arising from internal sac, visible beneath virga and projecting into ostium.

Flight. — The hind wing is vestigial in all specimens examined.

Bionomics. — Members of this species have been taken at altitudes from 6,300 to 8,000 feet during July and August. Ball's data indicate *hilariola* has been taken: in leaf litter near temporary ponds in palm-oak-pine forest 13.9 mi. W. Chilpancingo, 6,300 feet; and under stones on damp open ground in area with remains of cloud forest next to intact cloud forest at Omiltemi, 7,300 feet.

Distribution and material examined (21 specimens). This species has been taken from only a small area in the vicinity of Chilpancingo and Omiltemi Guerrero (Fig. 143). Its restricted range may in part be explained by its vestigial hindwing.

9.4 *Notiobia (Anisotarsus) schlingeri* NEW SPECIES (Figs. 4, 75, 76, 141)

Holotype ♂ labeled: "Mex. Jalisco 12.4 mi. s. Tecalitlan 5,300' August 4, 1967", "Ball, T. L. Erwin, R. E. Leech collectors", "Holotype *Notiobia (Anisotarsus) schlingeri* Noonan".

Description. — Body length 9.5 mm.

Color. Specimen apparently with external color of mature beetle but slightly teneral as median lobe not completely sclerotized. Dorsum black except rufopiceous near antennal insertion. Venter and legs piceous except following rufopiceous: prosternum, mesosternum, antecoxal piece, forecoxa, foretrochanter, midcoxa, midtrochanter, hindcoxa, posterior margin of midtrochanter, fore- and midtarsi. Palpi infuscated. Antenna with segments I and II rufous, remaining rufopiceous to infuscated.

Head. Labral apex slightly emarginate medially. Clypeal apex moderately emarginate medially. Frons with fovea small, punctiform; microsculpture of isodiametric mesh, slightly

obsolescent medially. Width of narrowest part of gena less than that of widest part of first antennal segment (w. gena/w. of first antennal segment = 0.64 for both sides).

Thorax. Pronotum (Fig. 4) with posterior angle prominent; lateral margins slightly sinuate posteriorly (more evident on right side); lateral bead prominent; basal bead complete; basal fovea as in Fig. 4; microsculpture consisting of transverse, nearly obsolete mesh medially, elsewhere of isodiametric mesh. Prosternum glabrous except for scattered very short hairs near anterior and lateral margins. Mesosternum with few scattered short hairs. Metasternum with scattered setae in region of midcoxa.

Legs. Midtarsus with segments II to IV laterally expanded and spongy pubescent beneath. Dorsum of foretarsus with few short setae. Dorsum of mid- and hindtarsus glabrous.

Elytron. Humerus obtusely angulate, without tooth; interval III with setigerous puncture at apical 1/3; subapical sinuation slight.

Abdomen. Sternum VI with 2 pairs of ambulatory setae.

Genitalia. Median lobe (Figs. 75, 76) not completely hardened; apex short, blunt, bent ventrad distally. Internal sac in repose with large prominent spine visible in dorsum of median lobe.

Allotype. Female. Same locality and collectors as holotype. Body length 9.08 mm. Fore- and midtarsi same color as rest of legs; sternum VI rufotestaceous; microsculpture of frons slightly more prominent; w. gena/w. of first antennal segment = 0.66; small, shallow outer basal fovea present on pronotum; microsculpture of pronotum more prominent medially and not as transversely stretched; fore- and midtarsi not laterally expanded or spongy pubescent beneath; humerus with prominent tooth; apex abdominal tergum VIII angulate; genitalia as in those of other *Anisotarsus* females; otherwise same as holotype.

Paratypes and variation. (all paratypes with same collectors as for holotype unless otherwise noted). One ♂, Mexico, Guerrero, Omiltemi, 7,300' VII. 14-15 1966, Ball-Whitehead; 1 ♂, 2 ♀♀, Mex. Michoacan, 1.1 mi. E. Angahuan, 7,500' nr. Paricutin, August 13, 1967; 1 ♀, Mexico, Michoacan, 1.3 mi. E. Comanja, 6,600' Rte. 15, VII. 30 1966, black light; 1 ♀ Mex. Jalisco, El Rincon, 30.5 mi. N.W. Los Volcanes, 5,400', August 10, 1967; 1 ♀, Mexico, Jalisco, 7.6 mi. S. Mazamitla, 5,700', Rte. 110, VIII. 6 1966, George E. Ball, D. R. Whitehead collectors; 1 ♂ with same data as holotype; 1 ♂, Temascaltepec, Distrito Federal, G. B. Hinton, 1931. The paratypes range in body length from 8.3 to 9.5 mm. The color is the same as in the holotype except that: the piceous areas listed for the holotype are testaceous to rufotestaceous in some specimens; midtarsus of some specimens testaceous to rufotestaceous; and dorsum in some specimens with slight purple tinge. The form of the pronotum is about the same as for the holotype, but the side varies within populations from moderately sinuate to non-sinuate in the posterior half, and the outer basal fovea varies from absent to present as a shallow depression. The microsculpture of the pronotum is slightly different in males and females as outlined in the description of the holotype and allotype. The humeral angle bears a prominent tooth in all females except the one from 7.6 mi. S. Mazamitla (lacks any evidence of tooth) and is without a tooth in all males.

Deposition of type material. — The holotype and allotype are deposited at MCZ and the paratypes at CAS, MCZ, and UASM.

Derivation of name. — It gives me great pleasure to name this species after Evert Schlänger who has given me constant encouragement and help during this study and during my years as a graduate student.

Discussion. — This species is most similar in appearance to *nitidipennis* but is distinguished by its different distribution and by morphological characters given in the key.

Bionomics. — Members of *schlingeri* have been taken in July and August, and at altitudes ranging from 5,300 to 7,500 feet. Ball's data indicate they have been found: under stones on loam soil of clay and gravel in open cleared places adjacent to forest intergrading from oak and pine to cloud forest at Omiltemi, 7,300 feet; in oak-pine litter on red-sand-clay soil near top of east side of north-facing ravine forested with oaks and pines 12.4 mi. S. Tecalitlan, 5,300 feet; in a forest of pines with some oaks and ground of volcanic ash 1.1 mi. E. Angahuan, 7,500 feet; under cover in clear area of oak-pine forest in vicinity of old logging camp at El Rincon, 30.5 mi. N.W. Los Volcanes, 5,400 feet; and under debris on reddish predominantly clay soil in open oak pine forest on slopes of ravine 7.6 mi. S. Mazamitla, 5,700 feet.

Distribution. — This species is found in central Mexico (Fig. 141).

9.5 *Notiobia (Anisotarsus) nitidipennis* (LeConte)

(Figs. 16, 39, 73, 74, 135)

Eurytrichus nitidipennis LeConte, 1848: 388. [Holotype (MCZ), ♂ labeled: orange disc without lettering, "504", "TYPE 5963", "E. nitidipennis Lec.". TYPE LOCALITY: Georgia as originally cited].

Anisotarsus cephalus Casey, 1914: 215. [Holotype (USNM), ♀ labeled: "Fla", "Casey bequest 1925", "TYPE USNM 47978", "cephalus Csy.". TYPE LOCALITY: Florida as originally cited. NEW SYNONYMY].

Anisotarsus delicatus Casey, 1914: 214. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♀ labeled: "NC", "Casey bequest 1925", "TYPE USNM 47977", "delicatus Csy". TYPE LOCALITY: Asheville, North Carolina as originally cited].

Anisotarsus tenuitarsis Casey, 1914: 215. [Lectotype (USNM), here designated, ♂ labeled: "Fla", "Casey bequest 1925", "TYPE USNM 47979", "tenuitarsis Csy". Additional label added stating: "LECTOTYPE Anisotarsus tenuitarsis Casey By G. R. Noonan". TYPE LOCALITY: Lake Worth, Florida as originally cited. NEW SYNONYMY].

Harpalus conspectus Casey, 1924: 103. [Holotype examined and synonymized by Lindroth (1968). TYPE LOCALITY: Mt. Royal, Quebec, Canada].

Harpalus agitabilis Casey, 1924: 104. [Holotype (USNM), ♂ examined by G. E. Ball. TYPE LOCALITY: District of Columbia as originally cited. NEW SYNONYMY].

Description. — Body length 5.9 to 8.2 mm.

Color. Dorsum dark piceous to black, in most specimens with prominent greenish or aeneous tinge; elytral suture, epipleuron, and margins of labrum and pronotum rufescent or testaceous in most specimens. Venter with apex of abdominal sternum VI rufescent or testaceous in most specimens; remainder piceous to black. Legs testaceous to rufotestaceous. Antenna with first segment testaceous to rufotestaceous, remaining various.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex slightly to moderately broadly emarginate medially. Frons with fovea obsolescent; microsculpture of isodiametric mesh. Head moderately to relatively large but with eye smaller, less protruding than in related species (Fig. 39). Gena as in *terminata*.

Thorax. Pronotum (Figs. 16, 39) with posterior angle varied from subdentate (Fig. 16) to rounded but prominent (Fig. 39); sides strongly convergent basally, rectilinear or faintly sinuate; lateral depression slightly evident near middle; basal bead complete in most specimens; basal fovea obsolescent; microsculpture of isodiametric mesh with tendency to become obsolete and transversely elongated medially. Prosternum pubescent. Proepisternum with scattered setae anteriorly. Mesosternum sparsely pubescent in some specimens. Metasternum with scattered pubescence.

Legs. As in *terminata*.

Elytron. As in *terminata*.

Abdomen. Sternum VI of ♂ with 1 or 2 pairs of ambulatory setae.

Male genitalia. Median lobe (Figs. 73, 74) with apex short, bluntly to nearly acutely rounded at tip. Internal sac in repose with large slender spine visible in distal region of membranous area of dorsum; everted sac with the large slender spine located proximal to median lobe and with apical field of enlarged scales.

Variation. — The shape of the pronotal posterior angle shows a north-south cline. The angle tends to be prominent and projecting (Fig. 16) in specimens from Canada and northern United States and southward becomes progressively more rounded and less prominent.

Intrapopulational variation occurs in: body size and color; degree of emargination of labral and clypeal apices; and shape of apex of female abdominal tergum VIII. The relative size of the head varies somewhat, but I have not seen sufficiently large series from individual localities to determine whether this variation is inter- or intrapopulational.

Discussion. — The form *cephalus* was characterized by Casey (1914), who listed *nitidipennis* as a species not seen, as having a relatively large head. Van Emden (1953) apparently never saw the types of *cephalus* or *nitidipennis* and separated *cephalus* from *nitidipennis* by this character. Lindroth (1968) expressed doubt about the validity of *cephalus* as a separate species. Actually, the head varies from moderately to relatively large in *nitidipennis*, and the holotype of *cephalus* is clearly a member of this species. The form *delicatus* was also described by Casey in 1914 who as mentioned above was not familiar with *nitidipennis*. Van Emden (1953) and Lindroth (1968) treated it as conspecific with *nitidipennis*, and the lectotype and 5 paralectotypes are clearly members of *nitidipennis*. Casey (1914) also described *tenuitarsis* without being familiar with *nitidipennis*. Van Emden (1953) correctly treated *tenuitarsis* as conspecific with *cephalus*. *Harpalus agitabilis* was proposed by Casey (1924) on the basis of a single male holotype; G. E. Ball (personal communication) has examined this male holotype and found it conspecific with *nitidipennis*.

Flight. — Leng (1915) reported members of this species taken at light at Fort Myers, Florida on March 30 and April 22 and as common at light in Mobile Co., Alabama. Lindroth (1968) mentioned specimens appeared in great number among drift material on the shore of Lake Erie at Long Point, Ontario, Canada.

Bionomics. — I have seen specimens collected from February into November, and Blatchley (1910) reported specimens taken from April 9 to December 25 in Indiana. Blatchley also reported specimens as occurring beneath cover in sandy localities in Indiana. Leng (1915) cited specimens taken at Everglade, Florida in a grassy meadow with low bushes. Lindroth (1968) stated that Larson found specimens "on clearings with moss but little higher vegetation" in Quebec, Canada.

Distribution and material examined (142 specimens). I have seen specimens from southern Canada south into Florida and southwest into Texas (Fig. 135). Blatchley (1910) reported this species as being found in Indiana "Throughout the western half of State; frequent in the southern counties, rare northward." Van Emden (1953) reported seeing a single specimen labeled as being from Colorado. Lindroth (1968) and Leng (1915) reported specimens from several localities in Canada and Florida respectively, and these localities were used in constructing Fig. 135.

9.6 *Notiobia (Anisotarsus) maculicornis* (Chaudoir)
 (Figs. 9, 83, 84, 134)

Harpalus maculicornis Chaudoir, 1843: 787. [Lectotype (MNHP), here designated, ♂ labeled: "New Orleans", "Ex Musaeo Chaudoir". Additional label added stating: "LECTOTYPE *Harpalus maculicornis* Chaudoir By G. R. Noonan". TYPE LOCALITY: New Orleans, Louisiana as originally cited].

Harpalus patronus Casey, 1914: 89. [Holotype (USNM), ♀ examined by G. E. Ball. TYPE LOCALITY: Morgan City, Louisiana, as originally cited. NEW SYNONYMY].

Anisodactylus depressus Notman, 1919: 236. [Lectotype (USNM), here designated, ♂ labeled: "Austin 10/20 Texas", "Anisodactylus depressus TYPE". Additional label added stating: "LECTOTYPE *Anisotarsus depressus* Notman By G. R. Noonan". TYPE LOCALITY: Austin, Texas as originally cited. NEW SYNONYMY].

Description. — Body length 12.7 to 13.1 mm.

Color. Dorsum and venter black to piceous. Legs and palpi rufopiceous to black. Antenna with segment I rufous; segment II rufous in most specimens, rufopiceous to piceous in some specimens; segment III piceous except in some specimens with rufous apex; segment IV testaceous to piceous; remaining segments in most specimens rufotestaceous except for median longitudinal black bar.

Head. Labral apex prominently emarginate medially. Clypeal apex broadly emarginate medially and in many specimens exposing base of labrum. Remainder as in *terminata*.

Thorax. Pronotum (Fig. 9) with posterior angle prominent, nearly right; lateral depression obsolete to prominent, wider and shallower basally; basal bead complete; basal fovea various, with punctures in most specimens; microsculpture of isodiametric mesh with slight tendency to become transversely elongated medially. Venter as in *terminata*.

Legs. As in *terminata*.

Elytron. Humerus somewhat angulate and in most specimens with vestigial tooth; intervals flat to slightly convex; punctuation of intervals as in *terminata* except interval IV may have several non-setigerous punctures; subapical sinuation moderate; sutural angle rounded; microsculpture of isodiametric mesh, slightly granulate in some ♀♀.

Abdomen. Venter as in *terminata*.

Male genitalia. Median lobe (Figs. 83, 84) with apex short, obtusely to acutely rounded at tip, in some specimens slightly removed to the right. Internal sac in repose with prominent spine visible through membranous area of dorsum of median lobe; everted sac with the large spine proximal to ostium and with distal field of small spines.

Discussion. — Notman proposed *depressus* as a new species of the genus *Anisodactylus*, and this form has apparently never been re-examined until now. The lectotype and single paralectotype are clearly members of the subgenus *Anisotarsus* and of the species *maculicornis*. *Harpalus patronus* was proposed by Casey (1914) on the basis of a single female holotype. G. E. Ball (personal communication) examined this female holotype and found it conspecific with *maculicornis*.

Flight. — Members of this species have been taken at light in a number of localities in Texas and Louisiana and seem to be ready fliers.

Bionomics. — Members of this species apparently are active throughout the year. Specimens have been taken on the docks at New Orleans.

Distribution and material examined (60 specimens). The species *maculicornis* is found in Texas and Oklahoma east of the 100th meridian and in Louisiana, Arkansas, and eastern Kansas (locality in Kansas not specified) (Fig. 134). I have also seen 1 male labeled as from Orient, Long Island, New York and 1 male labeled as from Riverhead,

Long Island, New York. Since these are the only 2 specimens recorded from Long Island, and this locality is far north of the established range of *maculicornis*, these 2 specimens may have been mislabeled.

9.7 *Notiobia (Anisotarsus) virescens* (Dejean)
(Figs. 2, 69, 70, 142)

Harpalus virescens Dejean, 1831: 839. [Holotype (MNHP), ♂ labeled: “♂”, “virescens. m in Mexico.”, “Harpalus”, “Höpfner”, “Ex Musaeo Chaudoir”, “Bates vidit 1881”. TYPE LOCALITY: Mexico originally cited, here restricted to 5.4 mi. E. Cuernavaca, 4,600', Morelos, Mexico].

Anisotarsus chloroderus H. W. Bates, 1882: 50. [Lectotype (BMNH), here designated, ♂ labeled: “Type H. T.”, “Puebla”, “Mexico Salle Coll.”, “B.C.A. Col. I. I. Anisotarsus chloroderus Bates”, “Anisotarsus chloroderus Bates ♂”. Additional labels added stating: “Lectotype” and “LECTOTYPE Anisotarsus chloroderus Bates By G. R. Noonan”. TYPE LOCALITY: Puebla and Cuernavaca originally cited, here restricted to Puebla, Puebla, Mexico].

Description. — Body length 7.7 to 10.4 mm.

Color. Dorsum green, blue, purple, cupreous, or bluish-purple; head, pronotum, and elytron of different colors in some specimens. Venter rufopiceous to piceous. Appendages rufous to piceous.

Head. As in *terminata*.

Thorax. Pronotum (Fig. 2) with posterior angle prominent but rounded; anterior angle obsolescent; lateral depression obsolescent; lateral bead fine apically; basal bead complete in most specimens; basal fovea shallow, not sharply defined, in most specimens somewhat oval in shape, separated from basal angle by convexity; microsculpture of prominent isodiametric mesh. Venter as in *terminata*.

Legs. As in *terminata*.

Elytron. Humerus in some specimens with vestigial tooth; remainder as in *terminata* except microsculpture of isodiametric granulate mesh.

Abdomen. Venter as in *terminata*.

Male genitalia. Median lobe (Figs. 69, 70) relatively narrow; apex short, bluntly rounded, not bent ventrad. Internal sac in repose with large prominent spine visible through membranous area of dorsum of median lobe; everted sac with the prominent large spine located proximal to median lobe and surface of sac with irregular varied distal field of scale-like spines and scales.

Variation. — Intrapopulational variation occurs in: body size and color; emargination of labral and clypeal apices; pubescence of prosternum and mesosternum; arrangement of scales and scale-like spines on internal sac.

Discussion. — Bates (1882) himself mentioned that he had doubts of *chloroderus* being distinct from *virescens*, and van Emden (1953) treated *chloroderus* as conspecific with *virescens*. The lectotype and 2 paralectotypes of *chloroderus* are clearly members of the species *virescens*.

Flight. — George Ball and D. R. Whitehead took 55 males and 28 females at black light 5.4 mi. E. Cuernavaca, and 1 male at light at Colima, Rte. 110. Members of the species are ready fliers.

Bionomics. — Members of this species have been collected in central and southern Mexico from June to September at altitudes ranging from 4,300 to 8,000 feet. Ball's data indicate *virescens* has been taken at black light 5.4 mi. E. Cuernavaca, 4,600 feet, in thorn forest on

old lava flow with substrated humus rich soil and outcropping volcanic rock.

Distribution and material examined (114 specimens). This species is found in central and southern Mexico (Fig. 142).

9.8 *Notiobia (Anisotarsus) picea* (LeConte)
(Figs. 7, 81, 82, 133)

Eurytrichus piceus LeConte, 1848: 388. [Holotype (MCZ), ♂ labeled: orange disc, "piceus 2" (see discussion of this holotype under notes). TYPE LOCALITY: NovEboraci originally cited, refers to New York (whether city or state not certain)].

Anisodactylus sayi Blatchley, 1910: 198. [Nomen novum for *piceus* LeConte, nec Menetries 1844].

Description. — Body length 8.1 to 11.3 mm.

Color. Dorsum rufopiceous to piceous, labrum in some specimens lighter than remainder. Venter rufous to rufopiceous. Legs, palpi, and antenna testaceous to rufotestaceous.

Head. Labral apex slightly emarginate medially. Clypeal apex slightly to moderately emarginate medially. Remainder as in *terminata*.

Thorax. Pronotum (Fig. 7) with posterior angle right; lateral depression prominent in most specimens but obsolescent in some; basal bead complete in most specimens; microsculpture obsolete medially, elsewhere of isodiametric mesh. Prosternum with varied fine short pubescence. Proepisternum of some specimens with few fine short setae on anterior portion. Mesosternum with sparse fine pubescence. Metasternum with setae in region of midcoxa.

Legs. Fore- and midtarsi of ♂ as in *terminata*. Dorsum of fore- and midtarsi sparsely pubescent. Dorsum of hindtarsus glabrous in most specimens.

Elytron. Humerus with slight tooth; intervals flat to slightly convex, with or without micropunctures; punctures of interval III as in *terminata*; subapical sinuation moderate.

Male genitalia. Median lobe (Figs. 81, 82) with apex short and tip rounded (dorsal view) in most specimens as in Fig. 81 but more angulate in some. Internal sac in repose with medium to large sized spine visible in region of ostium; everted sac with the spine located proximal to median lobe and with surface of sac bearing distal field of scale-like spines.

Discussion. — The LeConte collection at MCZ contains 1 male and 3 female specimens of *picea*. The first specimen is a female labeled: orange disc, "505", "Type 5962", "Eurytrichus piceus Lec.". It cannot be a type specimen since LeConte stated the original description was based on a single male. The second specimen is a male which fits the original description and must be the holotype since it is the only male in the series.

The name *sayi* was proposed by Blatchley (1910) as a replacement for *picea* LeConte which was temporarily preoccupied by *piceus* Menetries when the genus *Dicheirus* was regarded as a subgroup of *Anisodactylus* and *picea* LeConte by Blatchley as a member of *Anisodactylus*. It is now well established (Lindroth, 1968; Noonan 1968) that *piceus* Menetries belongs to *Dicheirus*, a valid separate genus, and that *picea* LeConte belongs in *Anisotarsus* (Lindroth, 1968).

Flight. — I have seen specimens taken at light from Pokagon State Park, 7 mi. N. Angola, Indiana; Ann Arbor, Michigan; and Houston, Texas. Lindroth (1968) reported examining 1 specimen which came to light at Trenton, Ontario.

Bionomics. — Members of this species have been collected from January to October but have been taken most frequently in July and August. I have seen one teneral female taken on July 17 in Michigan and several possibly teneral specimens taken during June at various

localities.

Lindroth (1968) reported the following ecological information: "At Belleville, Ont., common on a dry, sandy field; at Cowansville, Queb., in a dry sandpit with *Erigeron canadense*; in both places associated with *terminatus*." A female collected at Mineral Springs, Indiana bears a label stating it was found under shelter at the base of a pine tree in a tamarack swamp, and a female from Mason State Forest, Illinois, bears a label stating "bases of tufts grassland".

Distribution and material examined (220 specimens). This species is found from southeastern Canada to southeastern Texas (Fig. 133).

9.9 *Notiobia (Anisotarsus) flebilis* (LeConte)
(Figs. 15, 71, 72, 138)

Eurytrichus flebilis LeConte, 1863: 16. [Lectotype (MCZ), here designated ♂ labeled: gold disc with no lettering, "flebilis 2." Label added stating: "LECTOTYPE *Eurytrichus flebilis* LeC. By G. R. Noonan". TYPE LOCALITY: Cape San Lucas, Lower California as originally cited].

Anisotarsus castaneus Bates, 1884: 270. [Lectotype (BMNH), here designated, ♂ labeled: "Type H. T.", "Presidio, Mexico. Forrer.", "B.C.A. Col. I. 1. *Anisotarsus castaneus*, Bates.", "Anisotarsus castaneus Bates". Labels added stating: "Lectotype", and "LECTOTYPE *Anisotarsus castaneus* Bates By G. R. Noonan". TYPE LOCALITY: Presidio, Mexico as originally cited (according to Selander and Vaurie, 1962, refers to Presidio de (or near) Mazatlan, Sinaloa, Mexico. "A Forrer locality presumably referring either to the Rio Presidio or to a village on the river. The railroad crosses the Rio Presidio a few kilometers east of Mazatlan at 23° 10', 106° 14.'") NEW SYNONYMY].

Description. — Body length 7.3 to 10.9 mm.

Color. Dorsum and venter dull brown to rufopiceous. Appendages testaceous to rufotestaceous.

Head. As in *terminata*.

Thorax. Pronotum (Fig. 15) with posterior angle prominent but rounded; lateral depression of most specimens evident in region of lateral seta; basal bead complete; basal fovea shallow, in most specimens somewhat circular; outer fovea near posterior angle absent; microsculpture of isodiametric mesh with tendency towards transverse mesh medially. Prosternum completely pubescent or with glabrous median area; Remainder as in *terminata*.

Legs. As in *terminata*.

Elytron. Humerus without tooth; humeral angle obtuse; microsculpture of subgranulate isodiametric mesh; remainder as in *terminata*.

Male genitalia. Median lobe (Figs. 71, 72) with apex short, blunt. Internal sac in repose with elongate prominent spine visible in distal portion of membranous area of dorsum; everted sac with spine located proximal to median lobe, in some specimens with second much smaller medium sized spine located near the large spine, surface of sac with distal field of scales, microspines, and spine-like scales.

Variation. — I have not seen sufficient series of specimens from individual localities to be able to determine whether most of the observed variation is intra- or interpopulational. However, variations in body size and pubescence of the prosternum appear to be intra-populational.

Discussion. — Van Emden (1953) incorrectly applied the name "*flebilis castaneus*" to this species, termed a form from California and Arizona "*flebilis flebilis*" and a form found in southern United States and Mexico "*flebilis purpurascens*". However the lectotype of

flebilis is conspecific with the lectotype of *castaneus*, and both types are members of a species occurring in Guadalupe Island, southern Baja California, and the Mazatlan region of Mexico. The form found in California and Arizona and called “*flebilis flebilis*” by van Emden is conspecific with the form found in southern United States and Mexico which van Emden called “*flebilis purpurascens*”. These two forms thus constitute a valid species, *purpurascens*, separate from true *flebilis*.

The series of *flebilis* in the LeConte collection at MCZ consists of 5 specimens, each bearing a gold disc as the only locality label, and 2 specimens from Guadalupe Island. The first 5 appear to be members of the original type series while the 2 from Guadalupe Island clearly are not. The first specimen of *flebilis* is a female labeled: gold disc without any lettering, “Type 5961”, “E. *flebilis* Lec.”. (gold disc equals California according to LeConte’s color code). Since the median lobe of *flebilis* bears crucial taxonomic characters, I designate the second specimen, a male, as the lectotype.

Bionomics. — No information available other than Michelbacher and Ross collected a single female on July 28, 1938 at Mesquital, Lower California.

Distribution and material examined (60 specimens). This species has a disjunct distribution being found: on Guadalupe Island; in southern Baja California at Cape San Lucas, Mesquital, between San Jose del Cabo and Triunfo, and at San Jose del Cabo; and at Presidio de Mazatlan, Sinaloa, Mexico (Fig. 138).

9.10 *Notiobia (Anisotarsus) purpurascens* (H. W. Bates) (Figs. 3, 67, 68, 145)

Anisotarsus purpurascens H. W. Bates, 1882: 50. [Lectotype (BMNH), here designated, ♂ labeled: “Las Vigas, Mexico. Hoeg”, “B.C.A. Col. I. 1. *Anisotarsus purpurascens*, Bates”. Labels added stating: “Lectotype”, and “LECTOTYPE *Anisotarsus purpurascens* Bates By G. R. Noonan”. TYPE LOCALITY: Orizaba and Las Vigas, Mexico originally cited, here restricted to Las Vigas, Veracruz, Mexico].

Anisotarsus calathoides Casey, 1914: 212. [Lectotype (USNM), here designated, ♂ labeled: “Ari”, “Casey bequest 1925”, “Type USNM 47970”, “Calathoides Csy”. Label added stating: “LECTOTYPE *Anisotarsus calathoides* Casey By G. R. Noonan”. TYPE LOCALITY: Arizona as originally cited. NEW SYNONYMY].

Anisotarsus convexulus Casey, 1914: 210. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♀ labeled: “Tex”, “Casey bequest 1925”, “TYPE USNM 47968”, “convexus Csy”. TYPE LOCALITY: Galveston, Texas as originally cited. NEW SYNONYMY].

Anisotarsus extraneus Casey, 1914: 211. [Holotype (USNM), ♀ labeled: “Los Angeles Co. Cal.”, “Casey bequest 1925”, “TYPE USNM 47969”, “extraneus Csy”. TYPE LOCALITY: Los Angeles Co., California as originally cited. NEW SYNONYMY].

Anisotarsus inaudax Casey, 1914: 211. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♀ labeled: “Tex”, “Casey bequest 1925”, “TYPE USNM 47967”. TYPE LOCALITY: Galveston and westward nearly to El Paso originally cited by Casey, restricted to Galveston, Texas by Lindroth (1968). NEW SYNONYMY].

Description. — Body length 7.7 to 10.4 mm.

Color. Dorsum with labrum same color as remainder of head or somewhat lighter; remainder of head and pronotum rufopiceous to piceous or same color as elytron which may be bluish or purplish black or reddish purple; elytron rarely with faint greenish tinge. Venter rufopiceous to piceous. Appendages testaceous to rufous.

Head. As in *terminata*.

Thorax. Pronotum (Fig. 3) with posterior angle prominent but rounded; lateral depression evident in region of lateral seta in most specimens; basal bead complete in most specimens; basal fovea of most specimens consisting of shallow circular or elliptical depression; base of most specimens with outer fovea near posterior angle; microsculpture of isodiametric mesh with slight tendency towards transverse condition medially; shape of base various. Prosternum completely pubescent or with median glabrous area. Remainder of venter as in *terminata*.

Legs. As in *terminata*.

Elytron. Humerus without tooth; humeral angle varied from obtuse to acute; remainder as in *terminata*.

Abdomen. Sternum VI with 1 or 2 pairs of ambulatory setae in ♂.

Male genitalia. Median lobe (Figs. 67, 68) with relatively broad shaft; apex short and in most specimens acutely pointed. Internal sac in repose with large prominent spine visible in distal portion of dorsum of median lobe; everted sac with the large spine located proximal to median lobe and with surface of sac bearing irregular and varied mixture of scale-like spines and scales.

Variation. — Intrapopulational variation occurs in: degree of narrowing of basal portion of pronotum; presence or absence of outer fovea on pronotum; shape of basal fovea of pronotum; pubescence of prosternum; and body size.

Discussion. — This species was formerly known by the name "flebilis". However an examination of the lectotype of *flebilis* showed that it is actually a member of the species which was previously termed "castaneus" occurring in Baja California, Guadalupe Island and western Mexico. Since *flebilis* has priority, it must replace the name "castaneus", and the species occurring in western and southern United States and Mexico must be renamed with its senior synonym *purpurascens*.

The type series at the BMNH of the species *purpurascens* contains a male from Orizaba, Mexico bearing a type label. This type label apparently was added during routine curating because a lectotype has not previously been designated in publication for *purpurascens*. Since this male is in a state of decay and falling apart, I have decided to designate a male from Las Vigas, Mexico as lectotype.

The relationship of the form *calathoides* to *purpurascens* was not mentioned by Casey (1914) since he did not key out the latter species. However, the male lectotype and the paralectotypes of *calathoides* clearly fit my concept of the species *purpurascens*. Van Emden (1953) and Lindroth (1968) considered *convexus* conspecific with *picea*. However, the median area of the pronotum of the lectotype has prominent microsculpture whereas in *picea* the microsculpture is always obsolete medially. The lectotype and accompanying paralectotypes of *convexus* all agree with the characters described for *purpurascens*. The form *extraneus* was based on a single female from California. Casey's concept of its relationship to *purpurascens* can not be determined since he did not treat *purpurascens* in the key to species and listed *flebilis* (species name at time applied to *purpurascens*) as a species not seen by him. The holotype of *extraneus* agrees completely with my definition of the species *purpurascens*. The form *inaudax* was treated as conspecific with *picea* by van Emden (1953) and Lindroth (1968). However, its lectotype and paralectotypes cannot be members of that species for the same reasons mentioned concerning *convexus*. Rather they are members of the species *purpurascens*.

Flight. — I have examined 1 male and 2 females taken at light on May 7, 1938 at Anaheim, California and 1 male taken at light at San Diego, California on July 9, 1928. On September 2, 1964 I collected a female at black light 18 mi. S.W. Sinaloa, Mexico, and on July 10, 1964 I took a male at black light in Toll Road Public Campground, San

Bernardino Mountains, California. Moore (1937) reported many specimens of *extraneus* (synonym of *purpurascens*) taken at light in Mission Valley, California between August 20 and 25, 1928.

Bionomics. — Adults of this species apparently are present throughout the entire year. The species appears on the basis of collection data not to be common at any one locality since only 1 or 2 specimens are usually taken at a single locality and date.

On May 14, 1967 I collected a single female from under a board on the ground in the area of Newport Bay, near Newport, California. The ground beneath the board and within 3 to 4 feet of it consisted of moist clay bare of vegetation and cracked with deep fissures. The spot covered by the board was evidently earlier occupied by a temporary pond. The ground to within 3 to 4 feet of the board was covered with grass. The collecting site had scattered *Salix* sp., was in the bottom of a wash, and evidently received sun during most of the day. Several hours were spent collecting in this area, but no additional specimens were seen. Kenneth Cooper collected one female in a clump of cottonwoods and cattails near the borders of a permanent pond in Whitewater Canyon, (Riverside County) California on January 28, 1968.

Within mainland Mexico, George Ball and his students have taken this form: in litter under trees in canyon with sycamore, walnut, *Acacia*, agave, oaks, *bromeliads*, and Spanish Moss 14.8 mi. W. Linares, Rte. 60, 2,400 feet; under stones on sandy soil near small creek in deep gully 3.2 mi. S. Galeana; under stones on bare, chalky, muddy, abrasive ground near marl pond in area with desert type vegetation 3 mi. W. Galeana, 5,800 feet; under stone on river floodplain some distance from edge of Rio Salinas at Cienega de Flores, 1,200 feet; under cover in abandoned gravel pit near pond 11.7 mi. N. Montemorelos, Rte. 85, 1,550 feet; under cover on wet ground in vicinity of small stream in *Acacia*-grassland 5.3 mi. N. Aguascalientes, 6,100 feet; and under stones and in litter at edge of cornfield bordered by wet pine-oak forest at 33.7 mi. N.W. Los Volcanes, 5,400 feet.

Distribution and material examined (207 specimens). This species is found in central and southern California, southern United States and northern Mexico (Fig. 145).

9.11 *Notiobia (Anisotarsus) terminata* (Say), 1823 (Figs. 10, 11, 12, 13, 61, 62, 63, 64, 65, 66, 144)

Feronia terminata Say, 1823: 48. [Neotype (MCZ), designated by Lindroth (1969b), ♂ labeled: "Cleveland 7-15-27", "John Gehring Collection", "Neotype Feronia terminatus Say design. Lth.", "Anisotarsus terminatus det. Lindroth 68". TYPE LOCALITY: Cleveland, Ohio, as designated by Lindroth (1969b)].

Harpalus similis Say, 1823: 29. [Neotype (MCZ), designated by Lindroth (1969b), ♂ labeled: "Fla", "Collection of Frederick Allen Eddy", "Neotype Harpalus similis Say design. Lth.", "Anisotarsus similis Say (agilis Dejean) det. Lindroth 68". TYPE LOCALITY: North Carolina as originally designated by Say. NEW SYNONYMY].

Harpalus agilis Dejean, 1829: 357. [Lectotype (MNHP), here designated, ♂ labeled: "agilis. m in Amer. Bor", "similis Say.", "Leconte", "Ex Musaeo Chadoir". Label added stating "LECTOTYPE Harpalus agilis Dejean By G. R. Noonan". TYPE LOCALITY: "Amerique septenrionale" originally cited, here restricted to Archbold Biological Station, Highland Co., Florida. NEW SYNONYMY].

Harpalus ocreatus Say, 1834: 433. [Neotype (MCZ), here designated, ♂ labeled: "Mex., Chiapas. San Cristobal las Casas 7000' IX. 6. 65", "George E. Ball D. R. Whitehead collectors". Label added stating: "Neotype Harpalus ocreatus Say design. G. R. Noonan". (see discussion section for further information). TYPE LOCALITY: Mexico originally

cited, here restricted to San Cristobal las Casas, Chiapas, Mexico. NEW SYNONYMY]. *Harpalus testaceus* Haldeman, 1843: 302. [Type not located. TYPE LOCALITY: southeastern Pennsylvania as originally cited].

Anisotarsus foveicollis H. W. Bates, 1884: 269. [Lectotype (BMNH), here designated, ♂ labeled: "Type H. T.", "V. de Chiriqui, 4000-6000 ft. Champion.", "B.C.A. Col. I. 1. Anisotarsus foveicollis, Bates", "Anisotarsus foveicollis Bates ♂". Labels added stating: "Lectotype" and "LECTOTYPE Anisotarsus foveicollis Bates By G. R. Noonan". TYPE LOCALITY: Guatemala, Duenas, and Panama, Volcan de Chiriqui originally cited, here restricted to Volcan de Chiriqui, Chiriqui, Panama. NEW SYNONYMY].

Anisotarsus floridanus Casey, 1914: 214. [Lectotype (USNM), here designated, ♂ labeled: "Fla", "♂", "Casey bequest 1925", "TYPE USNM 47982", "floridanus Csy.". TYPE LOCALITY: Florida originally cited, here restricted to Archbold Biological Station, Highland Co., Florida. NEW SYNONYMY].

Anisotarsus subvirens Casey, 1914: 213. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♀ labeled: "Tex.", "Casey bequest 1925", "TYPE USNM 47976", "subvirens Csy". TYPE LOCALITY: Austin, Texas as originally cited. NEW SYNONYMY].

Anisotarsus angusticollis Casey, 1924: 137. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♂ labeled: "Mo.", "♂", "Casey bequest 1925", "TYPE USNM 47975". TYPE LOCALITY: St. Louis, Missouri as originally cited].

Anisotarsus connivens Casey, 1924: 139. [Holotype (USNM), ♂ labeled: "Marion County", "♂", "Casey bequest 1925", "TYPE USNM 47981", "connivens Csy.". TYPE LOCALITY: Marion County, Florida as originally cited. NEW SYNONYMY].

Anisotarsus fuscipennis Casey, 1924: 137. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♂ labeled: "Bayfld, Wis Wickham.", "Casey bequest 1925", "TYPE USNM 47971", "fuscipennis Csy.". TYPE LOCALITY: Bayfield, Wisconsin, and Marquette, Michigan originally cited, restricted to Bayfield, Wisconsin by Lindroth (1968)].

Anisotarsus hebes Casey, 1924: 136. [Lectotype (USNM), here designated, ♂ labeled: "Dallas Texas", "♂", "Casey bequest 1925", "TYPE USNM 47974", "hebes Casey". Label added stating: "LECTOTYPE Anisotarsus hebes Casey By G. R. Noonan". TYPE LOCALITY: Dallas, Texas as originally cited. NEW SYNONYMY].

Anisotarsus innerans Casey, 1924: 138. [Holotype (USNM), ♂ labeled: "Mo.", "♂", "Casey bequest 1925", "TYPE USNM 47966", "innerans Csy.". TYPE LOCALITY: St. Louis, Missouri as originally cited. NEW SYNONYMY].

Anisotarsus parallelus Casey, 1924: 138. [Holotype (USNM), ♀ labeled: "St L Mo", "Casey bequest 1925", "TYPE USNM 47973", "parallelus Csy.". TYPE LOCALITY: St. Louis, Missouri as originally cited. NEW SYNONYMY].

Anisotarsus subovalis Casey, 1924: 138. [Holotype (USNM), ♂ labeled: "Charleston Mo", "Casey bequest 1925", "TYPE USNM 47972", "subovalis Csy". TYPE LOCALITY: Charleston, Missouri as originally cited. NEW SYNONYMY].

Anisotarsus vernicatus Casey, 1924: 140. [Holotype (USNM), ♂ labeled: "Everglade Fla Apr. 6. '12", "Casey bequest 1925", "TYPE USNM 47980", "vernicatus Csy.". TYPE LOCALITY: Everglade Co., Florida as originally cited. NEW SYNONYMY].

Description. — Body length 6.3 to 9.6 mm.

Color. Dorsum with labrum rufous to piceous, anterior and lateral margins on most specimens lighter than remainder; clypeus rufous to piceous, anterior margin on most specimens lighter; remainder of head rufous to piceous, in some specimens with slight greenish tinge; pronotum rufous to piceous, lateral margin lighter in some specimens, disc in some specimens with slight greenish tinge; elytron rufous to piceous and in most specimens

with evident greenish tinge, in other specimens with faint aeneous tinge or completely lacking tinge. Venter rufous to piceous. Legs and palpi of most specimens testaceous, rufotestaceous in a few specimens. Antenna testaceous to rufous (in a few specimens some or all of the distal 9 segments darker).

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex slightly to moderately emarginate medially. Frons with fovea small, punctiform; microsculpture of isodiametric mesh. Narrowest part of gena narrower than maximum width of first segment of antenna.

Thorax. Pronotum (Figs. 10, 11, 12, 13) with sides slightly to strongly convergent basally; posterior angle prominent; lateral depression various; basal bead present laterally, in some specimens also present medially; outer fovea various; microsculpture of isodiametric mesh with tendency towards transverse mesh medially, in a few specimens nearly obsolete medially. Prosternum with varied pubescence. Proepisternum with scattered fine short setae near anterior margin. Proepimeron with scattered fine short setae near coxa. Mesosternum of some specimens sparsely pubescent. Metasternum irregularly pubescent except medially.

Legs. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath; segment I of many specimens with few adhesive hairs on inner ventral margin. Dorsum of tarsi sparsely pubescent in most specimens.

Elytron. Humerus without tooth; humeral angle of most specimens obtuse but in a few specimens more acute as in *nitidipennis*; intervals flat to slightly convex, with or without micropunctures; interval III with setigerous puncture at apical 1/3 or 1/4; subapical sinuation obsolescent; sutural angle rounded.

Male genitalia. Median lobe (Figs. 61, 62, 63, 64, 65, 66) varied from stout to narrow in form; apex pointed and bent slightly ventrad; internal sac in repose with large prominent spine visible through membranous area of dorsum of median lobe; everted sac with the large prominent spine located proximal to median lobe and with surface bearing varied mixture of scale-like spines and scales.

Variation. — This species shows complex geographical and intrapopulational variation. In regards to geographical variation, *terminata* shows a complex pattern of clinal variation. For the purposes of this discussion, 4 "morphs" (which are named and described below) can be recognized. Specimens from localities north of 40 degrees latitude (except for a few places in Nebraska and Iowa which contain members of southern morphs or intergrades with these morphs) are termed members of the "northern morph" and are characterized by: pronotum (Fig. 10) with a wide flattened lateral depression which is translucent and testaceous to rufotestaceous in color, and sides of pronotum only moderately convergent basally; and median lobe relatively stout in form and with internal sac spine located in proximal portion of dorsum when internal sac is in repose (Figs. 61, 62). There is a slight but still evident tendency for the lateral depression of the pronotum to become less pronounced from the north southward towards the 40th parallel. South of the 40th parallel, this reduction in prominence of the lateral depression rapidly becomes more apparent, the sides of the pronotum in specimens from some areas show an increasing tendency to be more strongly constricted basally, the median lobe becomes narrower in form, and the internal sac spine tends to be situated more distally inside the median lobe.

Specimens from south of the 40th parallel can be assigned to 1 of 4 morphs or else regarded as intergrades between these morphs. These 4 morphs are: the "northern morph" situated mainly north of the 40th parallel but with occasional specimens occurring as far south as the 35th parallel; the "Texas morph" centered in Texas; the "Florida morph" centered in Florida; and the "Mexico morph" centered in Mexico.

The Florida morph is characterized by: pronotum lacking lateral depression or at most with only an obsolescent one (Fig. 12); sides of pronotum strongly convergent basally in many specimens; and median lobe relatively slender and with spine of internal sac located distally in most specimens.

The Texas morph is characterized by: pronotum with lateral depression narrow and much less prominent than in specimens of the northern morph (Fig. 11); and median lobe which in most specimens is of the type described for the Florida morph (in some specimens the median lobe may be slightly stouter than in the Florida morph).

The Mexico morph is characterized by: pronotum either lacking lateral depression or having slight to moderate one; and sides of pronotum strongly convergent basally in most specimens. The form of the median lobe varies somewhat within members of this morph, and specimens from northern Mexico have a relatively slender median lobe with a distally located internal sac spine (Figs. 63, 64) as in the Texas and Florida morphs. Southward in Mexico the median lobe tends to become somewhat more stout (Figs. 65, 66) (but apparently never as stout as in the northern morph), and the internal sac spine tends to become more proximally located.

The Texas morph extends north into Kansas, Missouri, Tennessee, Virginia, North Carolina, Nebraska, and Iowa and intergrades in a north-southeastern clinal fashion with the northern morph in this broad area. Southward it intergrades in northern Mexico with members of the Mexican morph. It also intergrades with the Florida morph along the Gulf Coast from Mexico to the Mobile region of Alabama and at scattered localities in Alabama, Georgia, Tennessee, and South Carolina.

The Florida morph occupies all of Florida and extends north into Alabama, Georgia, South Carolina, Tennessee, and Missouri where it intergrades with the northern and Texas morph. This zone of intergradation is broad and there seems to be a visible cline running from north to southeast. The Florida morph also extends west along the Gulf Coast to nearly the Mexican border. From approximately Mobile westward there are found along the Gulf Coast specimens assignable to the Florida or Texas morph and specimens which are clearly intergrades between the 2 morphs. The Texas and Florida morphs thus intergrade over a wide area and seem to be part of a roughly east-west cline.

The Gulf Coast populations of *terminata* grade rapidly into the Mexico morph in northwestern Mexico in regards to pronotal characters. However, as mentioned above, the median lobe of specimens from northern Mexico tends to be similar to that found in the Florida and Texas morphs and changes more slowly than does the pronotum.

The species *terminata* also shows noteworthy intrapopulational variation. In the Texas, Florida, and Mexico morphs, the sides of the pronotum vary within populations from slightly to strongly convergent basally. The following additional characters exhibit intrapopulational variation throughout the species range: body size; color; degree of emargination of the labral and clypeal apices; presence, absence, and prominence of lateral depression of pronotum; presence medially of pronotal basal bead; prominence of pronotal microsculpture; pubescence of venter of body; presence or absence of spongy pubescence on venter of apex of segment I of male midtarsi; number of long setae on posterior margin of hind femur; degree of pubescence of dorsum of tarsi; shape of humeral angle of elytron; shape of elytron; and number and arrangement of scales and scale-like spines on internal sac.

Discussion. — In the synonymy of *terminata* I designated a neotype for *Harpalus ocreatus* Say. The insect collection of Say was entirely destroyed after his death except for a few specimens earlier sent to Dejean in France (Lindroth and Freitag, 1969b). I was unable to locate members of *ocreatus* in the Dejean collection. Therefore, in the interest of taxonomic stability it seems best to designate a neotype for *ocreatus*. The selection of the neotype was

based on the original description provided by Say and the concept of the form *ocreatus* followed by subsequent workers. The neotype has been deposited at MCZ as were the Say neotypes previously designated by Lindroth and Freitag (1969b).

The complex variation exhibited by *terminata* has caused several elements to be mistakenly treated as subspecies or species. The form *similis* was treated as a distinct species by van Emden (1953) apparently on the basis of pronotum only slightly narrowed basally and dorsum lacking greenish tinge. The name *agilis* has long been regarded as a synonym of *similis*. The type of *testaceus* has not been definitely located (although Lindroth, 1968, reports the existence of a possible type at MCZ), and previous workers have regarded it as conspecific with *terminata* apparently on the basis of specimens at some time labeled with the name *testaceus*. According to Casey (1924) *angusticollis* is distinguished as narrower and smaller than *terminata*. Van Emden (1953) listed *angusticollis* as possibly conspecific with *terminata*, and Lindroth (1968) correctly treated it as conspecific; its type is merely a small specimen of *terminata*. Another species proposed by Casey in 1924 was *connivens* which was distinguished from *floridanus* (which I regard as conspecific with *terminata*) by: relatively broader hind body or less parallel outline; piceous and not so metallic elytron; and dark rufous prothorax. Casey also proposed the name *fuscipennis* for four specimens which he felt differed from *testaceus* by: being "more abbreviated"; having piceous brown elytron; and having female specimens broader than male ones. The name *hebes* was applied by Casey to three specimens which he regarded as allied to *terminata* but shorter and broader and with relatively shorter and more inflated hind body. Van Emden (1953) tentatively listed *hebes* as a synonym of *terminata subvirescens*, and I treat *hebes* as conspecific with *terminata*. The name *parallelus* was used by Casey for a single female supposedly distinguished on the basis of denser and firmer integuments and elytral stria a little courser at the apex. Van Emden treated *parallelus* as conspecific with the species *picea*, but incorrectly since in the pronotum of the holotype of *parallelus* the microsculpture is not obsolete medially; the holotype of *parallelus* possesses the characters given above for *terminata* and is clearly a member of this species. Casey distinguished the form *subovalis* from *terminata* as smaller and having shorter and more oval elytra. Van Emden (1953) listed this form as possibly being conspecific with *terminata*, and the holotype has the characters listed above for *terminata* and is clearly a member of this species. The form *innerans* was cited by Casey as being allied to *agilis* which I regard as conspecific with *terminata*; the male holotype of *innerans* is a specimen somewhat intermediate between the northern and Florida morphs. Casey regarded *vernicatus* as being distinct from *floridanus* (which I regard as a member of *terminata*) on the basis of general body form; the holotype of *vernicatus* is clearly a member of the Florida morph of *terminata*.

Van Emden (1953) recognized 3 subspecies of *terminata* in addition to the nominate one: *subvirescens* from Texas and adjacent parts of Oklahoma and Kansas; *ocreatus* from Mexico and Guatemala; and *foevicollis* from Panama and Costa Rica. In addition, he treated as a separate species the form *floridanus* which he reported as occurring in Florida and several southeastern states. The forms *subvirescens*, *floridanus* and *ocreatus* correspond respectively to what I term the Texas, Florida, and Mexico morphs. As these morphs are merely segments of clines, they do not warrant separate specific status. I also think they do not warrant formal subspecific status since I believe this formal taxonomic category should be reserved for more distinctly geographically defined entities or preferably not used at all. The form *foevicollis* was distinguished by van Emden from *ocreatus* (the Mexico morph) on the basis of "Average size somewhat smaller, elytra narrower, less rounded at sides, brighter green in male". Van Emden himself admitted that the latter two forms were not very distinct. Body size and color vary within populations of *terminata* as, to a lesser degree, does

the shape of the elytron. I have not been able to find any combination of consistent taxonomic characters for separating specimens from Panama and Costa Rica and more northern locations, and there is no justifiable reason for retaining *foevicollis* as a valid subspecies.

Flight. — Specimens of this species have been taken frequently at lights in Canada, United States, and Mexico and are apparently ready fliers.

Bionomics. — Members of this species have been collected from March to October in Canada and northern United States and at higher elevations in the southern part of its range. In lowlands of the southeastern United States members have been taken year round. In Mexico specimens have been collected during all months but January and March. This gap may be due to a lack of collecting there during these months.

Lindroth (1968) reports that this species occurs on "dry, open, sandy ground with sparse vegetation, for instance on cultivated land and in gravel pits." Label data reveals that this species has been taken in the United States under a variety of different kinds of debris and stones on the ground.

This species is found in a variety of habitats in mainland Mexico. Summarizing information from Ball's data, *terminata* has been taken on the ground under stones or debris: in open pine, oak, or oak and pine forests; in or near agricultural areas; near water in several habitats; along roadsides; in vegetation near *Carex* marsh in semi-desert area at La Atascosa; in moist areas of high desert country; in cut-over cloud forest of mainly oak and pine with cacti, bromeliads, herbs and grass 21.8 mi. N. Juchatengo, 7,100 feet; and on flood-plain with bare, damp, sandy-clay soil about 50 feet from margin of Rio Sabinas Hidalgo, 7.9 mi. E. Sabinas Hidalgo, 800 feet. The various habitats in which *terminata* has been taken in mainland Mexico mostly all have the common feature of being relatively open land without dense forest cover.

It appears that *terminata* feeds at least in part on vegetable material. Blatchley (1910) mentioned that "in September 1903, this species was noted as very common on the heads of the fireweed (*Erechites hieracifolia* L.) in a deadening near Wyandotte Cave, Crawford County, where it was feeding on the seeds." A female at the USNM has pinned into its tray a card stating, "This carabid was reported causing considerable damage to milo seed planted at Lyons, Kansas, Rice Co. June 1945."

Johnson and Cameron (1969) reported interesting data on feeding habits of specimens found on golf courses in New York State. According to them, *terminata* was "A very active grass feeder in laboratory and field." Both sexes of the species ate seeds of the annual blue grass *Poa annua* L. in the laboratory. Gut contents of specimens from the field were composed of predominantly vegetable matter including grass blades, grass seed, and pollen. The species occasionally fed on larvae of *Hyperodes* (Coleoptera:Curculionidae) offered in the laboratory. When given a choice the laboratory specimens fed on "dry seed, seed in fresh panicles, and grass blades in that order." "The gut contents of field-collected specimens taken before mid-June were mostly vegetative portions of grass. . .; after the *P. annua* seed ripened in the field the gut contents were often predominantly seeds."

Distribution and material examined (2,665 specimens). The range of this species extends from southeastern Canada, through eastern United States, south along the mountains and highlands of Mexico, and into Central America as far south as Bugaba, Panama (Fig. 144). Four specimens have also been taken from Paget, Bermuda.

9.12 *Notiobia (Anisotarsus) lamprota* (H. W. Bates)
(Figs. 1, 77, 78, 136)

Anisotarsus lamprotus H. W. Bates, 1882: 51. [Holotype (BMNH), ♂ labeled: "Type H. T.",

"Veracruz", "Mexico Salle Coll.", "B.C.A. Col. I 1. *Anisotarsus lamprotus* Bates", "*Anisotarsus lamprotus* Bates". TYPE LOCALITY: Vera Cruz, Mexico as originally cited].

Description. — Body length 10.9 to 12.7 mm.

Color. Dorsum shiny (more so in ♂); head bluish green, bluish purple, less often purplish black; apex and sides of labrum slightly lighter in some specimens than remainder of head; pronotum same color as head but coloration more prominent in some specimens; elytron green, aeneous, or in some specimens cupreous. Venter, legs, palpi, and dorsum of hindtarsus rufopiceous to piceous. Antenna with first three segments at least in part rufopiceous or piceous and remaining segments reddish brown except for median longitudinal dark bar.

Head. Labral apex straight to moderately emarginate medially. Clypeal apex straight to moderately emarginate medially, base of labrum exposed in some specimens. Frons with fovea punctiform and relatively deep, in most specimens with linear medially directed impression; microsculpture of isodiametric mesh, obsolescent medially in some ♂♂. Narrowest part of gena wider than maximum width of first antennal segment. Antenna with relatively elongate segments; segments V to X 1.72 to 2.12 times as long as wide.

Thorax. Pronotum (Fig. 1) with posterior angle prominent; lateral depression present, but very narrow; lateral bead prominent, especially near posterior angle; basal bead complete; microsculpture of isodiametric mesh with tendency to become transverse medially. Prosternum, proepimeron near forecoxa, mesosternum, and metasternum each with short irregular pubescence in some specimens.

Legs. Dorsum of all tarsi sparsely pubescent.

Elytron. Humerus with or without small tooth; intervals flat to slightly convex; intervals III and V of some specimens and interval VII of all specimens with series of apical setigerous punctures; subapical sinuation slight; microsculpture of isodiametric prominent mesh in ♀, in most ♂♂ somewhat obsolescent medially and then appearing medially as fine lines, in some ♂♂ also of weak isodiametric mesh on median portions.

Male genitalia. Median lobe (Figs. 77, 78) relatively stout; apex bent slightly ventrad. Everted internal sac bearing small proximal field of scale-like spines.

Variation. — Intrapopulational variation occurs in body size and in pubescence of the venter. One male from 2.5 mi. W. Sontecomapan has an extra pronotal seta (illustrated in Fig. 1) slightly anterior to the usual one.

Flight. — George Ball and D. Whitehead collected a male and 3 females at black light 2.5 mi. W. Sontecomapan on June 5 and 20/1966.

Bionomics. — This species would seem to be rare, or at least very elusive, where it does occur, and I have not seen more than four specimens from a single locality. Specimens have been taken from May to October at altitudes ranging from 100 to 2,900 feet. Ball's data indicate specimens have been taken in: leaf litter on steep slopes in mountain rain forest containing large trees with buttresses, spiny palms, tree ferns, and vines at El Bastanal, near Coyame, elevation approximately 2,500 feet; among vegetation on rather dry sandy loam in banana-coffee plantation and also in leaf litter in cloud forest at Fortin de las Flores, 2,900 feet; and in moderately deep and wet litter in oak forest 5 mi. N.W. Cautla, 6,600 feet. It appears to be found in mesic, warm or nearly tropical environments.

Distribution and material examined (11 specimens). This species has been taken only from the state of Veracruz in Mexico (Fig. 136).

9.13 *Notiobia (Anisotarsus) mexicana* (Dejean)
(Figs. 5, 79, 80, 137)

Harpalus mexicanus Dejean, 1829: 288. [Lectotype (MNHP), here designated, ♂ labeled: "mexicanus. Klug in Mexica.", "♂", "Ex Musaeo Chaudoir". Label added stating: "LECTOTYPE *Harpalus mexicanus* Dejean By G. R. Noonan". TYPE LOCALITY: Mexico as originally cited].

Anisodactylus arizonae Casey, 1884: 6. [Holotype (USNM), ♂ labeled: "Ari.", "Casey bequest 1925", "TYPE USNM 47964", "arizonae type Casey". TYPE LOCALITY: Arizona as originally cited].

Stilboldius aztecanus Casey, 1914: 207. [Lectotype (USNM), here designated, ♀ labeled: "Guadalajara, Mexico VIII", "Casey bequest 1925", "aztecanus Casey", "TYPE USNM 47965". Label added stating: "LECTOTYPE *Stilboldius aztecanus* Casey By G. R. Noonan". TYPE LOCALITY: Guadalajara, Jalisco, Mexico as originally cited].

Description. — Body length 9.9 to 13.6 mm.

Color. Dorsum piceous to black, in most specimens with purple or bluish purple tinge, margins of labrum lighter than rest of dorsum in some specimens. Venter and legs rufopiceous to black. Palpi rufopiceous to piceous. Antenna rufous to piceous.

Head. Labral apex moderately emarginate medially. Clypeal apex straight to broadly emarginate medially, base of labrum exposed in some specimens. Frons as in *terminata*. Narrowest part of gena wider than maximum width of first antennal segment. Antenna with distal segments relatively stout, segments V to X 1.6 to 1.3 times as long as wide.

Thorax. Pronotum (Fig. 5) with posterior angle prominent, in most specimens slightly projected; side straight to sinuate before posterior angle; lateral depression obsolescent; lateral bead very prominent, especially near posterior angle; basal bead complete in most specimens; microsculpture of isodiametric mesh, somewhat less prominent medially. Prosternum, anterior part of proepisternum, mesosternum, mesepisternum near juncture with mesosternum, and metasternum in region of midcoxa with fine short pubescence in some specimens.

Legs. Dorsum of tarsi moderately to densely pubescent.

Elytron. Humerus of some specimens with vestigial tooth; intervals flat to slightly convex; intervals II to VII of most specimens with apical series of small setigerous punctures; subapical sinuation slight to obsolescent; sutural angle rounded.

Male genitalia. Median lobe (Figs. 79, 80) relatively stout; apex short, tip bent ventrad. Internal sac without discernible armature.

Variation. — Intrapopulational variation occurs in: body size, color and relative stoutness; emargination of labral and clypeal apices; shape of pronotal side before posterior angle; prominence of pronotal posterior angle; presence of pronotal basal bead medially; pubescence of thoracic venter; pubescence of tarsal dorsum; occurrence of vestigial tooth on elytral humerus; convexity of elytral intervals; punctuation of elytral intervals II to VII; and prominence of elytral subapical sinuation.

Discussion. — Casey (1884) described *arizonae* as a member of *Anisodactylus* apparently before he was familiar with the genera of Carabidae. In 1914 he treated it as a species of his new genus *Stilboldius* which he regarded as related to *Anisotarsus*. Van Emden (1953) found it indistinguishable from *mexicana* and treated it as conspecific, as did Lindroth (1968); the holotype of *arizonae* is clearly *mexicana*. Casey (1914) distinguished *aztecanus* by "much stouter in build and larger in size", but van Emden noted variation in body size and stoutness in Mexico, Guatemala, and Costa Rica. Body stoutness and size exhibit intrapopulational variation throughout the entire range of *mexicana*, and the lectotype of

aztecanus is merely a large, stout bodied example of this species.

Flight. — Members of this species do not appear to be ready fliers. I have examined: 1 female taken at light at Portal, Arizona; 1 female taken at UV light 11.6 mi. N. Ocozocuauitla, Mexico; and 1 male, 1 female taken at light in Jacala, Mexico. Since 2 is apparently the largest number of specimens taken at light in a single instance, it is possible that the above specimens crawled to the lights in question.

Bionomics. — Members of this species have been collected throughout the year at altitudes from 1,000 to 10,000 feet. Within the United States this species apparently is restricted to forests predominantly of pine, oak, and perhaps walnut in mountainous areas of Arizona, New Mexico, and Texas. I took 3 males and 3 females from under rocks on a grassy hillside with scattered oaks at a location 4.8 mi. W. Portal, Arizona. On September 7, 1964, I collected 11 males and 6 females at Bog Springs Public Campground, Madera Canyon, Arizona. The time of collecting was approximately 1:00 a.m., and the specimens were observed crawling over the ground. The area containing the specimens was heavily shaded by oak trees.

Elbert Sleeper has provided me with information concerning the vegetation in the La Laguna area of Baja California, and it is clear from this information that the species occurs there in the Laguna Woodland as defined by Axelrod (1958).

Within mainland Mexico the species *mexicana* occurs in a wide variety of habitats. Ball's data indicate it has been taken on the ground under debris or rocks: in forests of pine, oak, oak and pine, sycamore and walnut, and thorn; in or along edges of agricultural areas such as sugar cane and corn fields; along roadsides; by water in some habitats; and in moist areas with desert or semi-desert vegetation. It has also been taken under cover in gallery forest of *Celtis* trees 23.8 mi. N.E. Jacala, 5,100 feet.

Distribution and material examined (1,083 specimens). This species is primarily centered in highland areas of mainland Mexico but extends into mountainous areas of Arizona, New Mexico, Texas, south to Panama and occurs in the Laguna Mountains of Baja California (Fig. 137).

10 subgenus *Notiobia* Perty

Notiobia Perty, 1830: 13. [TYPE SPECIES: *Notiobia nebrioides* Perty, 1830, by monotypy].

Ragodactylus Chaudoir, 1835: 431. [TYPE SPECIES: *Ragodactylus brasiliensis* Chaudoir, 1835, by monotypy].

Batrachion Chevrolat, 1842: 500. [TYPE SPECIES: *Notiobia limbipennis*, here designated].

Batrachium Agassiz, 1846: 44. [emendation of *Batrachion*].

Description. — Body length 7.2 to 13.8 mm.

Color. Various.

Head. Frons with moderate to prominent fovea bearing in most specimens a clypeo-ocular prolongation. Eye of most species large and protruding. Width of narrowest part of gena less than maximum width of first antennal segment. Supra-antennal ridges slightly to strongly divergent anteriorly.

Thorax. Pronotum cordate and with base lobed in most species. Venter, unless otherwise stated, glabrous except for setae at apex of prosternal lobe.

Legs. Fore- and midtarsi of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Hindfemur with 2 long setae on posterior margin unless otherwise mentioned.

Elytron. Interval III with setigerous puncture in apical 1/3; interval VII with small

setigerous subocellate puncture near apex and slightly more proximal ocellate setigerous puncture.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae.

Discussion. — *Rhagodactylus* was proposed by Chaudoir (1835) for a single species, *brasiliensis* Chaudoir, 1835. This form was treated as conspecific with *nebrioides*, the type species of *Notiobia*, by Csiki (1932) apparently on the advice of Schuberger.

Dejean (1837, p. 50) listed *Batrachion* as a genus and cited 3 included species, *rana*, *rufipalpum*, and *chalconatum* as members of it. The genus name and the first two species names were apparently supplied by Chevrolat while *chalconatum* was proposed by Dejean. A description or indication was not provided for any of the 4 names cited by Dejean, and consequently his work has no nomenclatural status.

Chevrolat (1842: 500) mentioned Dejean's listing of *Batrachion* and the 3 species names and provided a description of the genus, but he did not provide a description or indication for any of the 3 species. Chevrolat is clearly the author of *Batrachion*. Csiki (1932) listed *Batrachion* as congeneric with *Notiobia*. Until now *Batrachion* has had no valid species. The Dejean collection at the MNHP contains 6 specimens labeled with the manuscript name *chalconatum*. These specimens are members of *Notiobia limbipennis*. In the interest of stability, I have designated *limbipennis* in the synonymy of the subgenus *Notiobia* as the type species of *Batrachion*.

The subgenus *Notiobia* has never been revised. Perty (1830), Bates (1882, 1884) and Putzeys (1878) proposed new species while various other workers have proposed (as members of other taxa) species now known to belong in it.

In this paper I have prepared a revision of the Mexican species of the subgenus along with a Central American form, *umbrifera*, which is closely related to *umbrata* found in Mexico. The named forms not revised by me are: *aeneola* Putzeys, 1878 *, described from Colombia; *aulica* (Dejean), 1829, seen by me from Bolivia and Brazil; *championi* H. W. Bates, 1882, described on basis of single female from Volcan de Chiriqui, Panama, holotype seen and probably conspecific with *jucunda* Putzeys; *chiriquensis* H. W. Bates, 1884, type series seen from Volcan de Chiriqui, Panama; *concolor* Putzeys, 1878, seen from Colombia, Ecuador, Panama; *disparilis* H. W. Bates, 1878, seen from Nicaragua, Panama, and "Amazonas" which refers to one of 3 regions in Colombia, Peru, or northern Brazil; *dubia* Putzeys, 1878 *, recorded from Colombia; *incerta* H. W. Bates, 1882, seen from Costa Rica, Nicaragua, Panama; *jucunda* Putzeys, 1878, seen from Costa Rica, Colombia, Ecuador, and Peru; *longipennis* Putzeys, 1878, seen from Dominica, described from Colombia; *nebrioides* Perty, 1830, described from Brazil; *praeclera* Putzeys, 1878 *, described from Colombia; *ruficrura* (Brullé), 1838, saw type from Bolivia; *similis* Putzeys, 1878 *, described from Colombia; *transversicollis* Putzeys, 1878 *, described from Colombia; *viridula* (Dejean), 1829 *, transferred under name of *viridellus* Csiki, 1832: 1185, nom. nov. from *Harpalus* to *Notiobia* by van Emden (1953: 516), (*viridellus* proposed as replacement for *viridulus* (Dejean) which was preoccupied by *Harpalus viridulus* Fourcroy, 1785 but with transfer to *Notiobia* is no longer preoccupied) described on basis of single specimen from Brazil; and *wilkensi* (Chaudoir), 1837, transferred from *Harpalus* to *Notiobia* by van Emden (1953: 516), have seen specimens labeled as *wilkensi* from Central America and South America. According to unpublished notes of van Emden in BMNH *wilkensi* includes the following named subspecies, *pallipes* Bates, *concolor* Putzeys, *flavicincta* (Erichson), 1847 (tentatively transferred from *Anisotarsus* to *Notiobia* by van Emden, 1953: 520), and *subaurata* Bates (a variety of *pallipes* Bates). Further work is needed to verify the above conclusions. The form *concinna* (Erichson), 1847, was stated by van Emden (1953: 520) to probably belong in *Notiobia* rather than *Anisotarsus*; it will have to be listed as *incertae sedis* until the type is seen.

Key to the Mexican and one Central American species of the Subgenus *Notiobia*

Notes concerning the key.

The more difficult to understand characters used in the key are discussed here.

The color of body parts has been used in several couplets. Generally the color of a body part on a given specimen is easy to determine and is fairly stable even when examined under different lighting conditions. However, quite often a given structure may have a metallic reflection or tinge in addition to its basic color. This tinge is frequently affected by the type of light used to illuminate the structure. The degree of change produced in the tinge varies from species to species and from one body part to another. The most commonly noted variation in tinge is that when specimens are illuminated by an incandescent lamp and examined under the microscope the normal tinge is frequently not visible, and only the basic color is discernible. The tinges described in couplet 3 are best examined by using daylight or fluorescent lights giving illumination equivalent to daylight. A microscope need not be used in determining tinges described in couplet 3 since they cover relatively large portions of the beetle's dorsum. Specimens keying out to couplet 6 should first be examined under natural or equivalent light without the aid of a microscope. Then if their elytron does not show a greenish, bluish green, or aeneous tinge, they should be examined under a microscope to determine if the elytron is covered only in part with such a tinge. I have found that in specimens with the elytron only partly covered with such a tinge the tinge is visible even when an incandescent lamp is used for illumination. Similarly, specimens keying to couplet 15 are best examined under the microscope, and a normal incandescent lamp may be used.

Body size is mentioned in several couplets and in each instance has been measured as described in the section on measurements.

The length of the scutellar stria in relation to total elytral length is used to separate species in couplet 8. These lengths are measured as follows: length of scutellar stria along the dorsum from origin at an ocellate puncture near base of stria II to apical end; length of elytron along dorsum from apical tip of scutellum to apex of suture.

The presence or absence and prominence of a clypeo-ocular prolongation to the frontal fovea of the head are useful in separating several species. The clypeo-ocular prolongation is present in *obscura* but does not reach the eye and is often difficult to discern. Therefore, a few individuals of *obscura* may key to couplet 2 where they can be separated by re-examining the frontal fovea and noting the other characters given there.

In several species the internal sac of the male median lobe bears a large prominent elongate spine. When the internal sac is in repose inside the median lobe, this spine is found lying beneath the surface of the dorsal membranous area of the median lobe. In order to observe this spine, it is usually necessary that the median lobe be completely wetted with water. Also in some instances it is necessary to clear the median lobe by immersing it for 1 to 2 minutes in a hot solution of 5 to 10 percent potassium hydroxide.

*Key to Mexican and One Central American Species of the Subgenus *Notiobia**

1	Frontal fovea of head bearing clypeo-ocular prolongation which reaches eye in most specimens	4
-	Frontal fovea of head punctiform, lacking evident clypeo-ocular prolongation	2
2 (1)	Frontal fovea of head actually with faint short clypeo-ocular prolongation (may be difficult to discern); body length 7.2 to 9.5 mm; median lobe with prominent elongate spine visible beneath membranous area of dorsum (Fig. 99); apex of abdominal tergum VIII of ♀ rounded (Fig. 59)	(in part) <i>obscura</i> H. W. Bates, p. 332
-	Frontal fovea of head with clypeo-ocular prolongation completely absent; body	

length 9.9 to 13.8 mm; median lobe without prominent spine (Fig. 91); apex of abdominal tergum VIII of ♀ angulate (Fig. 55) 3

3 (2) Elytral intervals flat near base; AND Pronotum and elytron rufopiceous with slight greenish or aeneous tinge; AND pronotum and elytron always with same color or tinge *leiroides* H. W. Bates, p. 327

— Elytral intervals convex near base; AND pronotum and elytron of all Mexican and some Central American specimens purple or bluish purple; AND pronotum and elytron of differing colors in most Central American specimens, in a few specimens both pronotum and elytron bright bluish green
..... (in part) *parilis* H. W. Bates, p. 334

4 (1) Elytron with subapical sinuation prominent (especially in ♀); with spine at suture apex in many specimens (Figs. 47, 48) 5

— Elytron with subapical sinuation moderate to obsolescent (Figs. 49, 50); without spine at suture apex 6

5 (4) Body length 9.3 to 12.0 mm; apex of abdominal sternum VI of ♀ produced into ventrally projected spine (Fig. 131); median lobe with short apex (Figs. 95, 96) *limbipennis* H. W. Bates, p. 329

— Body length 7.3 to 8.4 mm; apex of abdominal sternum VI of ♀ unmodified; median lobe with elongate tapered apex (Figs. 97, 98)
..... (in part) *umbrifera* H. W. Bates, p. 336

6 (4) Elytron partly or wholly covered with greenish, bluish green, aeneous or cupreous tinge 11

— Elytron rufopiceous to black (if piceous to black then elytron may have purplish or bluish tinge) 7

7 (6) Pronotum with posterior angle rounded and side straight before it (Fig. 22); labral apex prominently emarginate medially (Fig. 57); apex of median lobe moderately long and with tip bent ventrad (Figs. 107, 108)
..... *ewarti* new species, p. 326

— Pronotum with posterior angle not rounded, subdenteate in most specimens, side straight or sinuate before it (Figs. 18, 20, 24, 25); labral apex at most moderately emarginate medially (Fig. 51); median lobe as in Figs. 91, 92, 93, 94, 99, 100, 105, 106) 8

8 (7) Scutellar stria of elytron very long, length scutellar stria/length elytron always greater than 0.3; median lobe with apex short, blunt, and lacking prominent internal sac spine (Fig. 105); body length 8.4 to 9.7 mm.
..... (in part) *umbrata* H. W. Bates, p. 335

— Scutellar stria of elytron of normal length, length scutellar stria/length elytron less than 0.2; median lobe with more tapered apex of moderate length and with prominent elongate spine beneath distal portion of dorsal membranous area (Figs. 93, 99) or median lobe lacking prominent spine beneath distal portion of dorsal membranous area (Fig. 91) and body length 11.3 to 13.1 mm. 9

9 (8) Median lobe without prominent elongate spine beneath distal portion of dorsal membranous area (Fig. 91); body length 11.3 to 13.1 mm; clypeo-ocular prolongation of frontal fovea of head not prominent
..... (in part) *parilis* H. W. Bates, p. 334

— Median lobe with prominent elongate spine beneath distal portion of dorsal membranous area (Figs. 93, 99); body length 7.2 to 10.9 mm; clypeo-ocular prolongation of frontal fovea of head various 10

10 (9) Frontal fovea of head with prominent clypeo-ocular prolongation which reaches

eye; AND/OR pronotum (Fig. 20) with wide lateral bead and prominent outward projected posterior angle *melaena* H. W. Bates, p. 331

Frontal fovea of head with faint clypeo-ocular prolongation which does not reach eye; AND/OR pronotum (Fig. 24) with lateral bead less wide and posterior angle not as prominent (in part) *obscura* H. W. Bates, p. 332

11 (6) Pronotal posterior angle rounded and pronotal side curved towards posterior angle or rectilinear, not sinuate before posterior angle (Fig. 19) (doubtful instances treated in both couplets) 12

— Pronotal posterior angle not rounded, subdente in most specimens and pronotal side sinuate before posterior angle in many specimens (Figs. 18, 21, 23, 24, 25) 13

12 (11) Hindfemur testaceous; median lobe constricted near apex in dorsal view (Fig. 101) (in part) *pallipes* H. W. Bates, p. 333

— Hindfemur piceous, less often rufopiceous; median lobe not constricted near apex (Fig. 103) *cooperi* new species, p. 325

13 (11) Dorsum of hindtarsus piceous to black; body length 11.3 to 13.1 mm. (in part) *parilis* H. W. Bates, p. 334

— Dorsum of hindtarsus testaceous to rufotestaceous; body length 7.2 to 9.7 mm. 14

14 (13) Frontal fovea of head with faint short clypeo-ocular prolongation which does not reach eye; median lobe as in Fig. 99, 100 (in part) *obscura* H. W. Bates, p. 332

— Frontal fovea of head with prominent clypeo-ocular prolongation which reaches eye 15

15 (14) Elytron with uniform greenish or cupreous tinge and uniform microsculpture; labral apex strongly emarginate medially (in part) *pallipes* H. W. Bates, p. 333

— Elytron with various shaped greenish or aeneous tinged macula on inner intervals; intervals VI to X near apex always piceous to rufopiceous and with microsculpture more prominent than in macula; labral apex not or only slightly emarginate medially 16

16 (15) Elytral macula in ♀ continuous, not divided; apex of abdominal tergum VIII of ♀ angulate (Fig. 54); median lobe with elongate tapered apex (Figs. 97, 98) (Panama and South America) (in part) *umbrifera* H. W. Bates, p. 336

— Elytral macula in ♀ reduced and divided into basal and apical fields; apex of abdominal tergum VIII of ♀ more rounded (Fig. 53); median lobe with short apex (Figs. 105, 106) (Mexico, Guatemala) (in part) *umbrata* H. W. Bates, p. 335

10.1 *Notiobia (N.) cooperi* NEW SPECIES

(Figs. 19, 58, 103, 104, 150)

Holotype. Male. Mexico, Nayarit, Tepic, VII-1-61, Collr: A. E. Michelbacher.

Description. — Body length 10.6 mm.

Color. Dorsum with labrum piceous; remainder of head and pronotum piceous with bluish tinge; elytron bluish green. Venter rufopiceous. Fore- and midlegs with coxae and trochanters rufotestaceous to rufous, remainder rufopiceous. Hindleg with trochanter rufous; coxa, femur, tibia rufopiceous; tarsus blackish; palpi rufopiceous. Antenna with first 3 segments infuscated medially, apices rufopiceous.

Head. Labral apex moderately emarginate medially. Clypeal apex broadly emarginate medially. Frons with fovea punctiform, bearing prominent clypeo-ocular prolongation to eye; microsculpture of isodiametric mesh; supra-antennal ridges only slightly divergent anteriorly.

Thorax. Pronotum (Fig. 19) with side evenly rounded to posterior angle; posterior angle slightly rounded; lateral depression shallow, becoming obsolete posteriorly and merging into area of basal fovea; lateral bead becoming very narrow anteriorly; basal bead complete; basal fovea indistinct, merged with lateral depression; microsculpture of isodiametric mesh, slightly transversely stretched medially. Pro- and mesosterna with few scattered short fine setae.

Legs. Foretibia with 4 spines on outer distal angle. Fore- and midtarsi with dorsum bearing scattered setae on segments I to IV and glabrous on segment V. Hindtarsus with dorsum glabrous.

Elytron. Intervals slightly convex; subapical sinuation slight; sutural angle broadly rounded; microsculpture of isodiametric mesh.

Genitalia. Median lobe (Figs. 103, 104) with apex obtusely rounded and tip bent ventrad. Inverted internal sac with elongate spine visible near distal end of median lobe membranous dorsal area.

Allotype. Female. Same label data as holotype. Body length 11.6 mm. Bluish tinge on dorsum of head and pronotum very slight; elytron piceous, with bluish green tinge which is less pronounced than in holotype. Labral apex slightly emarginate medially. Thorax with mesosternum bearing few scattered setae. Foretibia with outer distal angle bearing 5 spines. Fore- and midtarsus without laterally dilated segments. Dorsum of segments I to IV of foretarsus with scattered setae; dorsum of segment V of foretarsus and of all segments of mid- and hindtarsus glabrous. Elytron with microsculpture of granulate isodiametric mesh. Sternum VI of abdomen with 4 ambulatory setae. Abdominal tergum VIII with broadly rounded apex (Fig. 58). Remainder as in holotype.

Paratypes and variation. (all paratypes bear same label data as holotype). Four males, 3 females. The paratypes range in body length from 9.61 to 12.2 mm. The prominence of the bluish tinge of the head and pronotum and the bluish green color of the elytron varies from the condition described for the holotype to that in the allotype; however, the prominence is not correlated with sex in the paratypes. The labral apex varies from slightly to moderately emarginate medially. The number of spines on the outer distal angle of the foretibia varies from 3 to 5 and does not seem to be correlated with sex. The lateral dilation and dorsal pubescence of the tarsi in males and females is the same as described for the holotype and allotype respectively. The microsculpture of the elytron is as in holotype for males and as in allotype for females.

Deposition of type material. — The holotype and allotype are deposited in the California Academy of Sciences and the paratypes in the California Insect Survey Collection at the University of California, Berkeley.

Derivation of specific name. — It gives me great pleasure to name this species after Kenneth Cooper who has very kindly assisted me in this and other studies.

Distribution. — This species is known only from Tepic, Mexico (Fig. 150).

10.2 *Notiobia (n.) ewarti* NEW SPECIES

(Figs. 22, 57, 107, 108, 147)

Holotype. Male. Mexico, Veracruz, Coyame, Lake Catemaco, VII-1-10-63, D. R. Whitehead, Blk. It.

Description. — Body length 8.75 mm.

Color. Dorsum with labrum and clypeus rufotestaceous; remainder of head piceous with slight greenish tinge; pronotum rufopiceous; elytron piceous on disc, becoming rufopiceous near lateral margin. Venter generally piceous but with localized lighter areas. Legs (except rufopiceous hindcoxa) and palpi testaceous. Antennae testaceous. Holotype appears to be slightly teneral, and coloration may be somewhat darker in mature specimens.

Head. Labral apex prominently emarginate medially (Fig. 57). Clypeal apex broadly emarginate medially. Frons with fovea punctiform, bearing clypeo-ocular prolongation to eye; microsculpture of isodiametric mesh; surface with micropunctures; supra-antennal ridges moderately divergent anteriorly.

Thorax. Pronotum (Fig. 22) with sides arcuate anteriorly, convergent and rectilinear posteriorly; posterior angle rounded; lateral depression moderately prominent, complete, widened posteriorly and embracing area of basal fovea; basal bead complete; apical bead complete, but flattened and very fine medially; basal fovea indistinct, merged with lateral depression; microsculpture of isodiametric mesh, slightly transversely stretched medially; disc with micropunctures.

Legs. Foretibia with 2 spines on outer distal angle. Dorsum of tarsi as in holotype of *cooperi*.

Elytron. Scutellar stria moderately long and nearly reaching stria I; intervals very slightly convex and with micropunctures; subapical sinuation slight; sutural angle broadly rounded; microsculpture of isodiametric mesh, slightly stretched transversely in localized areas.

Genitalia. Median lobe (Figs. 107, 108) with apex elongate and tip curved ventrad. Inverted internal sac with large prominent elongate spine visible beneath membranous area of median lobe near ostium.

Paratype. One male, Mexico, 2 mi. S. Simojovel, Chiapas, VI-9-1969, J. M. Campbell. As in holotype except: body length 10 mm.; pronotum and elytron with slight greenish tinge; venter rufous; legs testaceous, rufotestaceous, or rufous; pronotal apical bead absent medially.

Deposition of type material. — The holotype is deposited now at UASM but will later be deposited at MCZ. The paratype is deposited in the Canadian National Collection at Ottawa, Canada.

Derivation of species name. — It gives me great pleasure to name this species after William Ewart who gave me considerable assistance while I was a graduate student.

Flight. — D. R. Whitehead took the holotype at black light at Lake Catemaco in July.

Bionomics. — The holotype was collected on July 1-10, 1963 and the paratype on June 9, 1969.

Distribution. — This species is known only from the region of Lake Catemaco, Veracruz, and 2 miles south of Simojovel, Chiapas (Fig. 147).

10.3 *Notiobia (N.) leiroides* H. W. Bates (Figs. 18, 55, 91, 92, 151)

Notiobia leiroides H. W. Bates, 1878a: 590. [Holotype (MNHP), ♀ labeled: "Vera Cruz", "Notiobia Leiroides Bates". Additional label added stating: "HOLOTYPE Notiobia leiroides Bates Det. G. Noonan 1970". TYPE LOCALITY: Veracruz, Veracruz, Mexico as originally cited].

Description. — Body length 9.9 to 13.8 mm.

Color. Dorsum with labrum and in some specimens anterior part of clypeus rufous, remainder rufopiceous and with greenish or brassy tinge. Venter rufopiceous to piceous. Legs

and palpi testaceous to rufopiceous. Antenna testaceous to rufopiceous; one or more of first 3 segments lighter than more distal ones in some specimens.

Head. Labral apex slightly or not at all emarginate. Clypeus with apex emarginate and in some specimens base of labrum exposed; surface wrinkled near apex in most specimens. Frons with fovea punctiform, lacking clypeo-ocular prolongation; microsculpture of isodiametric mesh, in some specimens obsolescent medially; supra-antennal ridges strongly divergent anteriorly.

Thorax. Pronotum (Fig. 18) with side slightly arcuate to rectilinear or sinuate before posterior angle; posterior angle acute to right and prominent; base lobed; lateral depression complete, becoming wider and shallower posteriorly, in most specimens embracing area of basal fovea; lateral bead becoming less prominent anteriorly; basal bead present laterally; basal fovea shallow, irregular, merging with lateral depression in most specimens; microsculpture of isodiametric mesh, slightly stretched transversely or nearly obsolete medially in some specimens. Mesosternum of some specimens with scattered setae near midcoxa. Metasternum with scattered pubescence near midcoxa.

Legs. Forefemur of most specimens with about 10 setae on posterior margin. Foretibia of most specimens with 5 to 7 spines on distal outer angle (number may vary from side to side on individual specimen). Hindfemur with 2 long setae on posterior margin. Dorsum of all tarsi sparsely pubescent.

Elytron. Intervals flat or slightly convex proximally, more convex distally; subapical sinuation present but not prominent; sutural angle broadly rounded; microsculpture in most specimens appearing as isodiametric slightly granulate mesh, in some specimens as isodiametric punctures at certain light angles.

Abdomen. Tergum VIII of ♀ with obtusely angulate apex (Fig. 55).

Male genitalia. Median lobe (Figs. 91, 92) relatively stout; weakly sclerotized virga on left side of ostium; apex obtusely rounded and with concave area on dorsum. Everted internal sac with 0 to 6 enlarged spine-like scales and with additional varied armature of smaller spines and scales.

Variation. — Intrapopulational variation occurs in: body length; coloration of anterior part of clypeus, legs, palpi, and antenna; emargination of labral and clypeal apices; prominence of microsculpture on frons; shape of pronotal base; pubescence of mesosternum; number of setae on posterior margin of forefemur; number of spines along distal outer angle of foretibia; pronotal microsculpture; convexity of elytral intervals; number of enlarged spine-like scales on internal sac; and arrangement and number of smaller spines and scales on internal sac. The variation in number of enlarged spine-like scales is especially noteworthy. In one population (from 3.2 mi. N. Zanatepec, Mexico) I dissected 4 males and found 2 specimens with internal sac lacking enlarged spine-like scales; 1 specimen with a single enlarged spine-like scale; and 1 with 6 enlarged spine-like scales.

Flight. — George Ball and his students took 2 males and 2 female at black light in a cut-over palm forest 12.8 mi. E. Manzanillo in August 1967.

Bionomics. — Members of *leiroides* have been collected from February to September and at altitudes from sea level to 4,600 feet. Ball's data indicate this species has been taken: in leaf litter near fig tree in tropical deciduous forest 5 mi. E. Tapanatepec, 800 feet; in deep leaf litter on sand to clay loam soil along dry stream bed in mainly tropical deciduous gallery forest 13.8 mi. E. San Blas, 200 feet; in litter of rain forest 2.5 mi. W. Sontecompan, 100 feet; in dry litter and under rocks in mango-zapote orchard at Santa Rosa, 3.2 mi. N. Zanatepec, 3,100 feet; under palm fronds and litter on shaded clay ground in palm forest 12.8 mi. E. Manzanillo, 100 feet; in cut-over palm forest 12.8 mi. E. Manzanillo, sea level; in leaf litter on river banks shaded by large deciduous trees in vicinity of Zanatepec; in leaf

litter in small dry creek bed surrounded by oak forest 37.7 mi. E. Comitan, 2,200 feet; in patch of litter on bare soil near small stream margined with large Mexican cypresses and herbaceous vegetation at Puente Ahuehueyec, 4,200 feet; in litter on dry ground at edge of corn field near small stream in area of former thorn forest at Puente Estudo; and under herbaceous vegetation along road 32.5 mi. E. Comitan, 2,200 feet.

Distribution and material examined (167 specimens). This species is known from Mexico, Guatemala, British Honduras, Nicaragua, and Costa Rica (Fig. 151).

10.4 *Notiobia (N.) limbipennis* H. W. Bates
(Figs. 17, 47, 48, 56, 95, 96, 131, 154)

Notiobia limbipennis H. W. Bates, 1878a: 590. [Possible holotype (MNHP), ♀ labeled: "Chontales Nicaragua", "Notiobia limbipennis Bates", "Ex-Musaeo H. W. Bates 1892". TYPE LOCALITY: "Chontales, Nicaragua" as originally cited by Bates. (according to Selander and Vaurie, 1962, Chontales is "Department to the east of Lago de Nicaragua. It formerly extended farther southward to what is now the department of Rio San Juan.")].

Notiobia sinuessa H. W. Bates, 1882: 56. [Lectotype (BMNH), here designated, ♂ labeled: "Type H. T.", "Type", "Zapote, Guatemala, C. Champion", "B.C.A. Col. I. I. Notiobia sinuessa, Bates ♂". Additional labels added stating: "Lectotype" and "LECTOTYPE Notiobia sinuessa Bates By G. R. Noonan". TYPE LOCALITY: Zapote, Guatemala as originally cited. (according to Selander and Vaurie, 1962, = El Zapote in department of Escuintla "Settlement about 12 km. northwest of Escuintla and south of Volcan de Fuego; 2000±feet; 14° 23', 90° 52'.") NEW SYNONYMY].

Description. — Body length 9.3 to 12.0 mm.

Color. Dorsum, except labrum and in some specimens anterior part of clypeus which lack tinges and may be lighter in color, with head and pronotum rufobrunneous, rufopiceous to piceous and with greenish, aeneous, or cupreous tinges (tinge may vary over surface of single head or pronotum); elytron of ♂ with greenish, aeneous, or cupreous tinged macula located on inner 7 to 9 intervals proximally and narrowed apically until only inner 2 to 4 intervals so occupied (tinge may vary over surface of single macula), remainder of elytron in ♂ rufopiceous to piceous; elytron in ♀ as in ♂ except macula of many specimens restricted to small apical area. Venter and legs rufobrunneous, rufopiceous to piceous, color may be varied on parts of the same structure. Palpi brunneous, testaceous to rufotestaceous, rufopiceous to piceous. Antenna of most specimens same color as palpi, first segment paler or not.

Head. Labral apex non-emarginate or slightly emarginate medially. Clypeus with apex lobed medially, straight, or moderately broadly emarginate, base of labrum exposed in some specimens; surface smooth to wrinkled. Frons with fovea punctiform, bearing prominent clypeo-ocular prolongation to eye; microsculpture of isodiametric mesh; supra-antennal ridges moderately divergent anteriorly; surface with numerous micropunctures.

Thorax. Pronotum (Fig. 17) with side straight before nearly right posterior angle; lateral depression complete, widened posteriorly and in many specimens embracing area of basal fovea; lateral bead very fine anteriorly; basal bead complete; basal fovea varied, shallow and forming part of posterior portion of lateral depression or deeper and separated from lateral depression by slight convexity; microsculpture as in *melaena*; surface with numerous micropunctures. Prosternum irregularly pubescent. Mesosternum glabrous or with irregular pubescence.

Legs. Forefemur with 4 to 7 setae on posterior margin. Foretibia with 4 to 7 spines on outer distal angle. Dorsum of fore- and midtarsi glabrous to sparsely pubescent. Dorsum of hindtarsus glabrous.

Elytron. Intervals of varied width, with micropunctures, flat to slightly convex proximally, slightly to moderately convex apically; subapical sinuation extremely prominent (in some specimens so prominent as to be angulate exteriorly) especially in ♀ (Figs. 47, 48); sutural angle narrowly rounded; suture with obsolescent to prominent upward projected spine; microsculpture of isodiametric mesh on macula, elsewhere of isodiametric granulate mesh.

Abdomen. Sternum VI of ♀ with apex medially elongated into slightly downward projected spine (Fig. 131). Tergum VIII of ♀ with angulate apex (Fig. 56).

Male genitalia. Median lobe (Figs. 95, 96) with moderately sclerotized virga present to left of ostium; apex short. Everted internal sac with varied fields of small scales and with or without varied field of enlarged spine-like scales; internal sac in repose with the field of enlarged spine-like scales visible or not in median area of ventral side of shaft.

Female genitalia. Stylus dorso-ventrally flattened, without concave area on dorso-lateral side.

Variation. — Intrapopulational variation occurs in: body size; body color; extent of macula on elytron; presence or absence of emargination of labral apex; shape of clypeal apex; surface texture of clypeus; pronotal lateral depression and basal fovea; mesosternal pubescence; number of setae on posterior margin of forefemur and number of spines on outer distal angle of foretibia (number of setae and spines may vary from side to side in same specimen); dorsal pubescence of fore- and midtarsi; convexity and relative width of elytral intervals; degree of prominence of elytral subapical sinuation and sutural spine; and armature of internal sac.

Discussion. — The possible holotype of *limbipennis* at the MNHP is a female. However, at the end of his original description Bates stated "Long 5½ lin. ♂. Hab. Chontales, Nicaragua (Belt)." The description refers to the elytron as having a prominent subapical sinuation which might indicate Bates was describing a female rather than a male since the subapical sinuation is more prominent in the female. The BMNH does not contain any specimens identifiable as types of *limbipennis*, and the Bates boxes in the Oberthür collection at MNHP contain a total of 2 specimens of *limbipennis*: the above-mentioned female and a female labeled "Bakia", "Ex-Musaeo H. W. Bates 1892". The female from Chontales, Nicaragua fits the original description, except for the portion stating the type to be a male, and probably is the true holotype.

The form *sinuessa* was according to Bates (1882) ". . . distinguished by its smaller size, darker coppery or brassy-brown colour (which is not changed to tawny on the alutaceous patches of the elytra), and by the upper end of the elytral sinuation not forming a sharp angle." These characters all vary within populations, and there is no valid reason to retain *sinuessa* as a separate species.

Flight. — George Ball and D. R. Whitehead took 2 males and 2 females at black light in a tropical montane forest 11.6 mi. N. Ocozocuautla in June 1966.

Bionomics. — Members of this species have been taken during June to August and at altitudes ranging from 140 to 2,700 feet. Ball's data indicate this species has been taken: under rock in partly shaded area in mixed deciduous woods 7.5 mi. E. Chiapa de Corzo, 2,700 feet; under herbaceous vegetation along road 32.5 mi. E. Comitan, 2,200 feet; and in forest with palms predominant, few very large bromeliads and rich understory of vegetation 5.7 mi. E. San Blas, 140 feet.

Distribution and material examined (82 specimens). This species has been taken from scattered localities in Mexico, Guatemala, Nicaragua, Costa Rica, Panama, (Fig. 154) and also from French Guiana, Peru, and Tobago.

10.5 *Notiobia (N.) melaena* H. W. Bates
 (Figs. 20, 59, 93, 94, 149)

Notiobia melaena H. W. Bates, 1882: 54. [Lectotype (BMNH), here designated, ♂ labeled: "Type H. T.", "Cordova", "Mexico Salle Coll.", "B.C.A. Col. I. 1. Notiobia melaena Bates", "Notiobia melaena Bates ♂". Additional labels added stating: "Lectotype" and "LECTOTYPE Notiobia melaena Bates By G. R. Noonan". TYPE LOCALITY: Cordova, Veracruz, Mexico as originally cited].

Notiobia aequata H. W. Bates, 1882: 54. [Holotype (BMNH), ♀ labeled: "Type H. T.", "Cordova", "Mexico, Salle Coll.", "Type", "B.C.A. I. 1. Notiobia aequata, Bates.", "Notiobia aequata Bates". TYPE LOCALITY: Cordova, Veracruz, Mexico as originally cited. NEW SYNONYMY].

Description. — Body length 10.4 to 10.9 mm.

Color. Dorsum with labrum rufous, remainder black, some specimens with purple or violaceous tinge on dorsum. Venter rufopiceous to black. Foreleg rufous to black. Midleg with tarsus and trochanter of most specimens rufous and remainder black. Hindleg rufous to black except tarsus not darker than rufopiceous. Palpi rufotestaceous. Antenna with first 4 segments independently varied from rufous to black except for rufous bases and apices.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex slightly to prominently broadly emarginate medially and in some specimens base of labrum exposed. Frons with fovea punctiform, bearing prominent clypeo-ocular prolongation to eye; microsculpture of isodiametric mesh, in some specimens obsolescent medially; supra-antennal ridges only slightly divergent anteriorly.

Thorax. Pronotum (Fig. 20) with side straight to prominently sinuate before posterior angle; posterior angle right to acute and slightly projected; lateral depression complete, shallower and wider posteriorly, in some specimens embracing area of basal fovea; lateral bead extremely prominent, especially posteriorly; basal bead complete; basal fovea various; microsculpture of isodiametric mesh, slightly stretched medially.

Legs. Forefemur with 4 to 7 setae on posterior margin. Foretibia with 2 spines in ♂ and 3 to 5 spines in ♀ on outer distal angle (number of setae on femur and number of spines on tibia in ♀ may vary from side to side on individual specimen). Dorsum of tarsi glabrous except for occasional spine-like seta.

Elytron. Intervlas flat to slightly convex; subapical sinuation slight; sutural angle broadly rounded; microsculpture of isodiametric or transversely stretched mesh.

Abdomen. Tergum VIII of ♀ with obtusely rounded apex (Fig. 59).

Male genitalia. Median lobe (Figs. 93, 94) with apex bent slightly ventrad. Internal sac in repose with prominent elongate spine visible beneath membranous dorsal area of median lobe; everted sac with the prominent elongate spine proximal to median lobe and with small scattered spine-like scales.

Discussion. — The form *aequata* was proposed by Bates as having elytral intervals flatter and posterior angle of pronotum more prominent. As noted in the description these characters vary within the species *melaena*, and the type of *aequata* falls within the normal limits of variation of these characters in *melaena*.

Flight. — George Ball and D. R. Whitehead took 1 female *melaena* at black light 11.6 mi. N. Ocozocuautla in a tropical montane forest in JUNE, and D. R. Whitehead took 1 male by black light at Fortin de las Flores in June.

Bionomics. — Specimens of *melaena* have been taken in June, August to October and at altitudes from 2,900 to 5,000 feet. Ball's data indicate they have been taken: in leaf litter near banks of river in partly cut-over evergreen tropical forest at Fortin de las Flores, 2,900

feet; and under rotten log near big elephant ear plant in heavily shaded section of oak-sweet gum forest at Sierra de Guatemala, 8.1 mi. W. Encino.

Distribution and material examined (22 specimens). This species occurs in southern Mexico and Guatemala (Fig. 149).

10.6 *Notiobia (N.) obscura* H. W. Bates

(Figs. 24, 50, 51, 99, 100, 152)

Notiobia obscura H. W. Bates, 1882: 53. [Lectotype (BMNH), here designated, ♀ labeled: "Playa Vicente, Mexico. Salle. Coll", "B.C.A. Col. I. 1. Notiobia obscura, Bates.". Additional labels added stating: "Lectotype" and "LECTOTYPE Notiobia obscura Bates By G. R. Noonan". TYPE LOCALITY: Playa Vicente, Veracruz, Mexico as originally cited]. Var. *virens* H. W. Bates, 1882: 53.

Description. — Body length 7.2 to 9.5 mm.

Color. Dorsum with labrum and in some specimens anterior part of clypeus rufous to piceous; remainder of head and pronotum rufopiceous to piceous, in some specimens with slight cupreous or greenish tinge; elytron rufopiceous to piceous, in most specimens with distinct greenish or aeneous tinge. Venter rufopiceous to piceous. Legs of most specimens testaceous to rufotestaceous, in a few specimens rufopiceous, in some specimens with coxa, trochanter, base of femur, and tarsus lighter than other parts. Palpi rufotestaceous to rufopiceous. Antenna rufotestaceous.

Head. Labral apex slightly emarginate medially (Fig. 51). Clypeus with apex slightly to moderately broadly emarginate, in some specimens base of labrum exposed; surface slightly wrinkled. Frons with fovea punctiform, bearing faint short clypeo-ocular prolongation not reaching eye; microsculpture of isodiametric mesh, obsolescent medially; supra-antennal ridges only slightly divergent anteriorly.

Thorax. Pronotum (Fig. 24) with side slightly to moderately sinuate before posterior angle; posterior angle prominent, slightly to moderately projected, acute; base lobed; lateral depression shallow, incomplete, becoming obsolete posteriorly; lateral bead becoming less prominent anteriorly; basal bead complete; basal fovea varied, obsolete in some specimens; microsculpture of isodiametric mesh, obsolescent medially in some specimens.

Legs. Forefemur with 3 to 7 setae on posterior margin. Foretibia with 2 spines in ♂ and 4 in ♀ on outer distal margin. Dorsum of laterally dilated segments in ♂ fore- and midtarsi glabrous to sparsely pubescent, dorsum of segment V glabrous. Dorsum of all tarsi in ♀ and hindtarsus in ♂ glabrous.

Elytron. Intervals flat; subapical sinuation slight (Fig. 50); sutural angle rounded; microsculpture of isodiametric mesh.

Abdomen. Tergum VIII of ♀ with obtusely rounded apex as in *melaena*.

Male genitalia. Median lobe as in Figs. 99, 100. Internal sac in repose with prominent elongate spine visible in distal portion of dorsal membranous area of median lobe; everted sac with the prominent elongate spine located proximal to median lobe and with fields of small spine-like scales.

Discussion. — The name *virens* was mentioned by Bates as being based on specimens from Cordova, Mexico, labeled with this name in the Salle collection. These specimens were distinguished from other *obscura* by having the pronotal posterior angle slightly more prominent. However, variation occurs in the prominence of this angle, and there is no reason to validate the name *virens*.

Bionomics. — Members of *obscura* have been taken in February, May, and July and at altitudes from 1,000 to 6,000 feet. Ball's data indicate specimens have been taken: in deep

litter on black rich loam soil in cool, densely shaded ravine with tropical vegetation 33.7 mi. N. Huixtla, 6,000 feet; under banana log in banana plantation located in pine-oak zone 18.4 mi. S. Suchixtepec, 4,500 feet; and in damp, deep litter in vicinity of dried pond inside cloud forest with very dense canopy 16.9 mi. S. Valle Nacional, 3,600 feet.

Distribution and material examined (15 specimens). This species is found in southern Mexico (Fig. 152).

10.7 *Notiobia (N.) pallipes* H. W. Bates
(Figs. 21, 52, 101, 102, 156)

Notiobia pallipes H. W. Bates, 1882: 53. [Lectotype (BMNH), here designated, ♂ labeled: "Type H. T.", "Type", "Oaxaca, Mexico. Hooge.", "B.C.A. Col. I. 1. Notiobia pallipes, Bates", "Notiobia pallipes Bates ♂". Additional labels added stating: "Lectotype" and "LECTOTYPE Notiobia pallipes pallipes Bates By G. R. Noonan". TYPE LOCALITY: Type material originally stated to be from Cordova, Jalapa, and Oaxaca in Mexico. Type locality here restricted to Oaxaca, Oaxaca, Mexico].

Var. *subaurata* H. W. Bates, 1882: 53. [Holotype (BMNH), ♂ labeled: "Holotype", "Capetillo, Guatemala, G. C. Champion.", "B.C.A. Col. I. 1. Notiobia pallipes, v. subaurata, Bates", "Notiobia pallipes v. subaurata". Additional label added stating: "Holotype Notiobia pallipes subaurata Bates det. G. Noonan 1970". TYPE LOCALITY: Capetillo, Guatemala as originally cited. NEW SYNONYMY].

Description. — Body length 8.2 to 9.5 mm.

Color. Dorsum with labrum and in some specimens anterior part of clypeus rufous or rufopiceous, remainder rufopiceous, with prominent greenish tinge. Venter rufopiceous. Legs with coxae testaceous, brunneous, or rufopiceous, remainder testaceous. Palpi testaceous. Antenna testaceous to rufotestaceous.

Head. Labral apex prominently emarginate medially. Clypeal apex broadly emarginate medially and in some specimens base of labrum exposed. Frons with fovea punctiform, bearing prominent clypeo-ocular prolongation to eye; microsculpture of isodiametric mesh; supra-antennal ridges strongly divergent anteriorly.

Thorax. Pronotum (Fig. 21) with side rectilinear or sinuate before posterior angle; posterior angle right and prominent or obtuse and not prominent, slightly projected in some specimens; lateral depression complete, shallower and slightly wider posteriorly; basal fovea shallow, not distinctly defined; microsculpture of isodiametric mesh, in some specimens slightly transversely stretched medially. Metasternum with few short fine setae near junction with mesosternum.

Legs. Forefemur with 3 to 5 setae on posterior margin. Foretibia with 2 in ♂ and 3 to 4 spines in ♀ on outer distal angle (number of spines may vary from side to side on individual ♀). Dorsum of tarsi glabrous except for occasional spine-like seta.

Elytron. Intervals flat except slightly convex near apex; subapical sinuation slight; sutural angle broadly rounded; microsculpture of isodiametric mesh.

Abdomen. Tergum VIII of ♀ with obtusely rounded apex (Fig. 52).

Male genitalia. Median lobe (Figs. 101, 102) with shaft markedly constricted (in dorsal view) just before apex. Internal sac in repose with prominent elongate spine visible beneath distal portion of median lobe membranous dorsal area; everted sac with the prominent elongate spine proximally located and with fields of scales and small spines.

Variation. — Intrapopulational variation occurs in: body length; coloration of anterior part of clypeus, coxae, and antenna; emargination of clypeal apex; shape of pronotal side; pubescence of metasternum; number of setae on posterior margin of forefemur; and number

of spines on outer angle of foretibia in females.

Discussion. — The form *subaurata* was described on the basis of a single male from Capetillo, Guatemala and characterized by having the pronotal side sinuate just before the acute and slightly projected posterior angle. The few specimens I have seen from Guatemala do indeed have this type of pronotum. Most Mexican specimens have the posterior angle more obtuse and non-projected while the pronotal side is usually straight or very slightly sinuate before the posterior angle. However, the shape of this angle and the sinuation of the side vary within populations in Mexico. Therefore, I do not recognize *subaurata* as a valid subspecies.

Flight. — George Ball and D. R. Whitehead have taken this species at black light in June: at Fortin de las Flores; and in a tropical montane forest 11.6 mi. N. Ocozocuautla.

Bionomics. — Members of *pallipes* have been taken in January, March to June, and August and at altitudes from 2,624 to 4,700 feet. Ball's data indicate specimens have been taken: from bromeliads on south-facing slope of pasture in badly cut-over area once probably predominantly of *Liquidamber* forest 10.4 mi. S. W. Huatusco, 4,700 feet; from bromeliad in partly cut-over tropical evergreen forest at Fortin de las Flores, 2,900 feet; and by washing deep, rich leaf litter located within a few feet of river at Fortin de las Flores.

Distribution and material examined (63 specimens). This species occurs in southern Mexico (Fig. 156). I have also seen 2 specimens from Guatemala.

10.8 *Notiobia (N.) parilis* H. W. Bates
(Fig. 153)

Notiobia parilis H. W. Bates, 1878 a: 590. [Lectotype (MNHP), here designated, ♂ labeled: "Chontales Nicaragua". Additional label added stating: "LECTOTYPE Notiobia parilis Bates By G. R. Noonan". TYPE LOCALITY: Chontales, Nicaragua as originally cited (according to Selander and Vaurie 1962, = department to east of Lago de Nicaragua, formerly extended farther southward to what is now department of Rio San Juan)].

Description. — Body length 11.3 to 13.1 mm.

Color. Mexican morph. Dorsum with labrum and anterior part of clypeus in some specimens rufous to rufopiceous, in other specimens piceous and with distinct purple tinge as in rest of dorsum. Venter and legs rufopiceous to piceous. Palpi rufopiceous to piceous or infuscated. Antenna rufopiceous to piceous; one or more of first 3 segments may be lighter than more distal ones.

Color. Panamanian morph. Dorsum with labrum and in some specimens anterior part of clypeus rufous to rufopiceous or else clypeus same color as rest of dorsum of head; head and pronotum green, aeneous, or cupreous. Elytron purple or bluish purple. Venter and legs piceous in most specimens, rufopiceous in a few specimens, with slight irregular greenish tinge. Palpi same as in Mexican morph. Antenna piceous in most specimens, rufopiceous in a few specimens; one or more of first 3 segments may be lighter than more distal ones.

Head. As in *leiroides*, except clypeo-ocular prolongation present in some specimens. Thorax. As in *leiroides*.

Legs. As in *leiroides*.

Elytron. As in *leiroides* except that intervals of elytron are moderately convex proximally.

Abdomen. As in *leiroides*.

Male genitalia. Median lobe as in *leiroides*. Internal sac with armature of small spines and scales as in *leiroides*; no enlarged spine-like scales present.

Variation. — I did not examine enough specimens to evaluate all of the variation shown by this species. However, it is apparent that intrapopulational variation exists in the: degree of

emargination of clypeal apex and shape of basal part of pronotum.

The coloration of the body shows interesting geographical variation. Specimens from Mexico have the dorsum with the proximal part of the head and all of the pronotum and elytron bearing a conspicuous purplish tinge. Specimens with this color state are here referred to as the "Mexican morph". The Mexican morph extends into Central America, and the following specimens from there belong to this morph: 1 male, 3 females from Chontales, Nicaragua; 1 female from San Jose, Costa Rica; and 2 males, 1 female from Costa Rica. In Central America, variation in body color occurs and there is found a second form, here termed the "Panamanian morph", in which the head and pronotum of most specimens differ in color from the elytron. The venter and legs also have a faint irregular greenish tinge, and the appendages are usually darker in color than in the Mexican morph. Five color combinations are outlined in Table 1 (p. 428). These color combinations show a definite tendency to intergrade, and it is often difficult to decide in which category a specimen belongs; and more than one color combination may occur at a single locality. Thus, this color variation is probably intrapopulational in nature; additional collecting is needed to completely determine the nature of this variation.

Discussion. — The BMNH contains 1 *parilis* labeled: "Type H. T.", "Playa Vicente", "Mexico Salle Coll", "B.C.A. Col. I. 1. *Notiobia parilis*, Bates.", "*Notiobia parilis* ♂ Bates". This specimen cannot be a syntype since it is not from the type locality originally cited by Bates.

Flight. — George Ball and his students have collected *parilis* at black light in a tropical montane forest 11.6 mi. N. Ocozocuautla in June 1966 and at Fortin de las Flores in May 1966.

Bionomics. — Members of this species have been collected in February, April to June, August to September, and at altitudes from 0-100 to 3,200 feet. Ball's data indicate *parilis* has been taken: in leaf litter of lowland rain forests in the vicinity of Sontecompan and at the Palenque ruins; in leaf litter near banks of river in partly cut-over tropical evergreen forest at Fortin de las Flores, 2,900 feet; and in densely shaded leaf litter in mountain rain forest at San Quintin, Sierra de la Colmena, approximately 300-700 feet.

Distribution and material examined (72 specimens). This species is known from southern Mexico, Central America, (Fig. 153) and São Paulo (whether city or province not certain) Brazil. I have seen 1 male labeled "Amazones" which probably refers to 1 of 3 areas named "Amazonas" in Colombia, northern Brazil, or Peru.

10.9 *Notiobia (N.) umbrata* H. W. Bates (Figs. 25, 49, 53, 105, 106, 155)

Notiobia umbrata H. W. Bates, 1882: 55. [Lectotype (BMNH), here designated, ♂ labeled: "Zapote, Guatemala C. Champion", "B.C.A. Col. I. 1. *Notiobia umbrata* Bates.", "*Notiobia umbrata* Bates". Additional labels added stating: "Lectotype" and "LECTOTYPE *Notiobia umbrata* Bates By G. R. Noonan". TYPE LOCALITY: Zapote, Guatemala as originally cited (according to Selander and Vaurie, 1962 = El Zapote, Department of Escuintla, "settlement about 12 km. northwest of Escuintla and south of Volcan de Fuego; 2000± feet; 14° 23', 90° 52'").]

Description. — Body length 8.4 to 9.7 mm.

Color. Dorsum with labrum and anterior part of clypeus rufous to rufopiceous; remainder of head and pronotum rufopiceous to piceous and with distinct prominent greenish tinge or slightly less prominent cupreous tinge; elytron of ♂ with greenish tinged macula in most specimens on inner 9 intervals proximally and narrowed apically until only inner 2 to 4 inter-

vals so covered; remainder of elytron of ♂ rufopiceous to piceous; elytron of ♀ completely rufopiceous to piceous or with various proximal and distal greenish tinged maculae on inner intervals. Venter rufopiceous to piceous; abdominal sterna (especially apical ones) of most specimens with sides testaceous or brunneous, apex of sternum VI of most specimens testaceous or brunneous. Legs testaceous except hindcoxa of most specimens rufopiceous. Palpi testaceous to brunneous. Antenna same color as palpi.

Head. Labral apex not emarginate. Clypeus with apex broadly emarginate medially or wavy, base of labrum exposed in most specimens; surface wrinkled near apex. Frons with fovea punctiform, bearing clypeo-ocular prolongation to eye; microsculpture of isodiametric mesh; supra-antennal ridges strongly divergent anteriorly.

Thorax. Pronotum (Fig. 25) with side straight or very slightly sinuate before posterior angle; posterior angle acute to slightly obtuse; base lobed; lateral depression complete, widened posteriorly; lateral bead less prominent anteriorly; basal bead complete; basal fovea shallow, not distinctly defined; microsculpture of isodiametric mesh. Prosternum sparsely pubescent with short fine setae.

Legs. Forefemur with 3 to 7 setae on posterior margin. Foretibia with 3 to 4 spines on outer distal angle (number of spines may vary from side to side on individual specimen). Dorsum of segments I to IV of fore- and midtarsi of ♂ pubescent; dorsum of segment V of ♂ glabrous. Dorsum of all tarsi of ♀ and of hindtarsus of ♂ glabrous.

Elytron. Scutellar stria extremely long (length scutellar stria/length elytron greater than 0.3); intervals flat except slightly convex near apex; subapical sinuation slight to moderate; sutural angle broadly rounded; microsculpture of isodiametric mesh, granulate isodiametric mesh, or isodiametric punctures.

Abdomen. Tergum VIII of ♀ with obtusely rounded apex (Fig. 53).

Male genitalia. Median lobe (Figs. 105, 106) with apex short. Internal sac not examined in everted position due to lack of mature ♂♂; no armature visible through walls of median lobe.

Flight. — George Ball and D. R. Whitehead have taken *umbrata* at black light: in a tropical montane forest 11.6 mi. N. Ocozocuautla in June; and in a montane rain forest in hills 5 to 6 miles away from Lake Catemaco in July.

Bionomics. — Members of *umbrata* have been collected from June to July and at altitudes from 100 to 4,700 feet. Ball's data indicate specimens have been taken: in deep leaf litter on sandy to clay loam soil along dry stream bed in mainly tropical deciduous gallery forest 0.9 mi. N. Frontera Comalapa, 2,100 feet; inside densely shaded lowland rain forest 2.5 mi. W. Sontecompan, 100 feet; and in densely shaded leaf litter in lowland rain forest at Palenque ruins, 400 feet.

Distribution and material examined (17 specimens). This species occurs in southern Mexico and Guatemala (Fig. 155).

10.10 *Notiobia (N.) umbrifera* H. W. Bates (Figs. 23, 54, 97, 98, 148)

Notiobia umbrifera H. W. Bates, 1884: 271. [Lectotype (BMNH), here designated, ♂ originally glued on single card with ♀ paralectotype. Lectotype now pinned and bearing following labels formerly on pin holding both specimens: "Type H. T.", "Bugaba Panama Champion.", "B.C.A. Col. I. 1. *Notiobia umbrifera* Bates.", "*Notiobia umbrifera* Bates". Additional labels added stating: "Lectotype" and "LECTOTYPE *Notiobia umbrifera* Bates By G. R. Noonan". Paralectotype ♀ now bears handwritten label duplicating information on original labels and handwritten label stating that ♀ was formerly on same card as lectotype. TYPE LOCALITY: Bugaba, Panama and Upper Amazons, South America

originally cited, here restricted to Bugaba, Panama (Bugaba, according to Selander and Vaurie, 1962, = settlement about 22 km. northwest of David, 1,000 feet, $8^{\circ} 28'$, $82^{\circ} 38'$].

Description. — Body length 7.3 to 8.4 mm.

Color. Dorsum with labrum and anterior part of clypeus testaceous, rufous to rufopiceous; remainder of head and pronotum rufopiceous to piceous and with greenish or aeneous tinge; elytron of both sexes with greenish or aeneous tinged macula occupying in most specimens inner 8 to 9 intervals proximally, narrowed apically until only inner 2 to 4 intervals so covered, remainder of elytron rufous to rufopiceous. Venter with thorax rufous to piceous; abdominal sterna testaceous to rufous to brunneous medially, rufopiceous to piceous laterally in most specimens. Legs as in *umbrata*. Palpi testaceous to rufotestaceous, rufous to rufopiceous, or brunneous. Antenna same color as palpi.

Head. As in *umbrata* except dorsum wrinkled near clypeus.

Thorax. Pronotum (Fig. 23) with side straight or very slightly sinuate before prominent posterior angle; base lobed; lateral depression not prominent, wider and obsolete posteriorly; lateral bead narrowed anteriorly; basal bead present laterally, obsolete medially; basal fovea obsolete; microsculpture of isodiametric mesh, in some specimens slightly transversely stretched medially.

Legs. Forefemur with 3 to 7 setae on posterior margin. Foretibia with 3 to 5 spines on outer distal angle (number of setae on femur and number of spines on tibial outer angle may vary from side to side on individual specimen). Dorsum of segments I to IV of ♂ fore- and midtarsi pubescent; dorsum of segment V glabrous. Dorsum of all tarsi in ♀ and of hindtarsus in ♂ glabrous.

Elytron. Scutellar stria moderately long; intervals flat except near apex; subapical sinuation moderate; sutural angle broadly rounded; microsculpture of isodiametric mesh on macula and of granulate isodiametric mesh or isodiametric punctures elsewhere.

Abdomen. Tergum VIII of ♀ with angulate apex. (Fig. 54).

Male genitalia. Median lobe (Figs. 97, 98) with apex very elongate, in many specimens curved leftward. Internal sac in repose bearing prominent large spine visible beneath dorsal membranous area of median lobe; dissected internal sac bearing several elongate small spines in addition to the prominent large spine.

Female genitalia. Stylus compressed medio-laterally and somewhat lobe-like.

Variation. — Intrapopulational variation occurs in: body color; emargination of clypeal apex; shape of pronotal base; number of setae on posterior margin of forefemur; number of spines along distal outer margin of foretibia; pronotal microsculpture; elytral microsculpture; and curvature of median lobe apex.

Flight. — Members of this species have been taken at lights on Barro Colorado Island, Canal Zone, Panama.

Bionomics. — All specimens bearing dated labels were collected between April and November.

Distribution and material examined (56 specimens). Bates (1884) cited specimens from Panama and Upper Amazons, South America. I have seen material only from Panama (Fig. 148), but additional collecting may reveal that it does extend into South America.

11 subgenus *Diatypus* Murray NEW STATUS
(Figs. 210, 211)

Diatypus Murray, 1858: 343. [TYPE SPECIES: *Diatypus dohrni* Murray, 1858 (according to Basilewsky, 1950)].

Dichiropsis Jeannel, 1946: 157. [TYPE SPECIES: *Anisodactylus picinus* Chaudoir, 1878, by

original designation].

Paradiatypus Basilewsky, 1950: 19. [TYPE SPECIES: *Diatypus smithi* Murray 1858, by original designation. NEW SYNONYMY].

Description. — Body of most specimens piceous to black, but in some specimens with metallic tinges on dorsum.

Head. Labral apex slightly to moderately emarginate medially. Frontal fovea punctiform, with or without clypeo-ocular prolongation. Eye large and protruding. Gena (except in few species of “*Paradiatypus*” species group) narrow with narrowest part between margin of eye and mouth much narrower than maximum width of first antennal segment. Ligula narrow and not expanded laterally at apex in “*Diatypus*” species group; broader and strongly expanded laterally at apex in “*Paradiatypus*” species group. Paraglossa wide and longer than ligula in “*Diatypus*” species group; narrow and shorter than ligula in “*Paradiatypus*” species group.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindtarsus with segment I shorter or equal to II + III. Dorsum of all tarsi glabrous. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals convex in most specimens; interval III with 3 to many dorsal setigerous punctures; interval VII with minute ocellate puncture at extreme apex and large prominent ocellate puncture slightly more proximally located.

Hind wing. Various in size.

Abdomen. Sternum VI of ♂ with 1 or 2 pairs of ambulatory setae.

Male genitalia. Median lobe with apex narrow, bearing “button”-like disc (Figs. 210, 211).

Discussion. — The reasons for regarding *Diatypus* as a subgenus of *Notiobia* rather than as a separate genus are reviewed in the discussion section on the genus *Notiobia*. Basilewsky (1950) provided a thorough review of why *Dichiropsis* must be regarded as congeneric with *Diatypus*, and I agree fully with him in this decision. Basilewsky (1950) proposed *Paradiatypus* as a subgenus of the then separate genus *Diatypus*. I here treat the former subgenus *Paradiatypus* as a species group of the subgenus *Diatypus*.

The subgenus is composed of 2 species groups defined by ligula and paraglossa characters listed in the genus description. The species of both groups are found in tropical portions of Africa. The 3 “*Diatypus*” group species are: *diffusus* (Klug), 1833; *dohrni* Murray, 1858 ♀*; and *picinus* (Chaudoir), 1878. The 7 “*Paradiatypus*” group species are: *bamboutensis* Basilewsky, 1948*; *elongensis* Basilewsky, 1948*; *feanus* Basilewsky, 1949*; *kivuensis* Burgeon, 1936 ♀*; *leonensis* Basilewsky, 1949 ♀*; *ruwenzoricus* Burgeon, 1936 ♀*; and *smithi* Murray, 1858 ♀*.

12 genus *Anisostichus* van Emden NEW STATUS (Fig. 175)

Anisostichus van Emden, 1953: 520. [(as subgenus of *Anisotarsus*) TYPE SPECIES: *Harpalus laevis* Curtis, 1839 by original designation].

Description. — Body length 6.3 to 8.6 mm.

Color. Various.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex slightly to moderately emarginate medially, in some specimens base of labrum exposed. Frons with obsolete or very small punctiform fovea lacking clypeo-ocular prolongation; microsculpture of isodiametric mesh (obsolete medially in *amoenus*); supra-antennal ridges slightly to moderately divergent anteriorly; narrowest width of gena wider than maximum width of first

antennal segment. Mentum with prominent tooth. Mentum and submentum fused, only groove indicating former separating suture (groove somewhat deeper in *octopunctatus* and *posticus*). Ligula (Fig. 175) narrow, not expanded at apex. Paraglossa (Fig. 175) subequal in length to ligula.

Thorax. Pronotum moderately convex; slightly cordate to rectangular in shape; base straight to slightly lobed; lateral depression obsolete; lateral bead complete, not prominent; basal bead complete in most specimens, obsolete medially; apical bead present laterally; basal fovea obsolescent; microsculpture of isodiametric mesh, slightly transversely stretched medially (except obsolete medially in *amoenus*). Prosternum irregularly, sparsely pubescent. Metasternum with or without scattered pubescence. Mesosternum of most specimens sparsely pubescent. Remainder of venter glabrous.

Legs. Foretibia with apical spur lanceolate. Hindfemur with 2 long setae on posterior margin, except 3 to 5 in *amoenus*. Hindtarsus with segment I shorter than II + III. Dorsum of all tarsi glabrous to pubescent. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments II to IV and also in some specimens apex of segment I laterally expanded and spongy pubescent beneath.

Elytron. Humerus with or without small tooth; scutellar stria long and capturing distal portion of stria I in many specimens; intervals flat to slightly convex; interval III with 3 to 6 setigerous punctures extended from apex to or nearly to base; interval VII with minute setigerous sub-ocellate puncture near apex and slightly more proximal ocellate puncture; sub-apical sinuation obsolescent; stria in *amoenus* weak or obsolescent except for first, normal in other species; microsculpture in *amoenus* of transverse mesh, in *laevis* and *octopunctatus* of isodiametric mesh, in *posticus* of slightly transverse isodiametric mesh.

Hind wing. Full and apparently functional in all species.

Abdomen. Sternum VI with 2 pairs of ambulatory setae in ♂, 1 pair in occasional specimens of *laevis*. Apex of ♀ tergum VIII obtusely angulate to broadly rounded.

Male genitalia. Median lobe with membranous area of dorsum reaching basal bulb in *octopunctatus* and *posticus*, short and not reaching basal bulb in *amoenus* and *laevis*. Internal sac in repose with elongate spine visible in region of ostium of median lobe.

Female genitalia. Valvifer similar to that of *Notiobia*; weakly sclerotized, slightly convex; lateral distal margin partly membranous and without discrete boundary.

Discussion. — This group was proposed as a subgenus of *Anisotarsus* by van Emden (1953). However it merits separate status from *Notiobia* (*s. str.*) and *Diatypus* because of the fused mentum and submentum. And the series of setigerous punctures on the third elytral interval distinguish its species from those of *Anisotarsus* and *Notiobia* (*s. str.*).

The 4 species of *Anisostichus* occur in temperate areas of South America and are: *amoenus* (Solier), 1849; *laevis* (Curtis), 1839; *octopunctatus* (Dejean), 1829, and *posticus* (Dejean), 1829. Van Emden (1953) provided a key to these species.

13 genus *Scybalicus* Schaum
(Figs. 183, 208, 209, 216)

Scybalicus Schaum, 1862: 118. [TYPE SPECIES: *Harpalus oblongiusculus* Dejean, 1829 by monotypy].

Apatelus Schaum, 1860: 560. [preoccupied by *Apatelus* Mulsant and Rev. 1859. TYPE SPECIES: *Harpalus oblongiusculus* Dejean, 1829, by monotypy].

Description. — Body length 12 to 14 mm. Body somewhat elongate in form and with dense pubescence.

Color. Body brown to black.

Head. Labral apex prominently emarginate medially. Frontal fovea varied (within species) from obsolete to moderate sized and deep, with or without slight clypeo-ocular prolongation. Antenna moderately long, exceeding pronotal base. Mentum with obtuse tooth. Mentum and submentum separated by complete transverse suture. Submentum with various setae of different length and thickness. Ligula slender; dorsal surface with several very fine short setae in *hirtus*, glabrous in *oblongiusculus*. Paraglossa slightly longer than ligula.

Thorax. Pronotum (Fig. 183) semicordate; lateral depression obsolescent; lateral bead present anteriorly but in many specimens obsolescent towards posterior angle; apical bead present only laterally; basal bead absent or suggestion of bead present laterally near posterior angle.

Legs. Foretibial apical spur dilated near base or angulate at sides. Foretarsus of ♂ with at least segment II to IV slightly laterally expanded and spongy pubescent beneath. Mid-tarsus of ♂ various. Hindtarsus with segment I as long or longer than II + III.

Elytron. Scutellar stria moderately long and in some specimens distally reaching stria I; all intervals densely pubescent.

Male genitalia. Median lobe of *oblongiusculus* (Figs. 208, 209) with apex deflected to right and bearing moderate apical disc; membranous area of dorsum somewhat indistinct; ventral surface unmodified.

Female genitalia. Valvifer (Fig. 216) moderately sclerotized, flattened, with several distal setae.

Discussion. — The genus *Scybalicus* contains 3 species: *biroi* Jedlicka, 1952*, described from Dijarbekir, Asia Minor; *kabylianus* Reiche, 1861*, found in mountains of northeastern Algeria and northwestern Tunisia; and *oblongiusculus* (Dejean), 1829, found in England, southern Europe, and northern Africa.

To prevent possible further confusion the form of the median lobe of *oblongiusculus* (Figs. 208, 209) will be briefly discussed here. Jeannel (1942a) described the ventral border as being equipped with a "sorte de carène lamelleuse longitudinale". As pointed out by Antoine (1959), and confirmed by myself the ventral border does not possess such a structure and is unmodified.

14-15 genus *Progonochaetus* G. Müller

Progonochaetus G. Müller, 1938: 245. [TYPE SPECIES: *Anisodactylus xanthopus* Dejean, 1829, by original designation].

Description. — Body length 9 to 11 mm.

Color. Body of most specimens black to piceous; elytron of some specimens with slight bronze tinge.

Head. Labral apex straight to moderately emarginate medially. Clypeal apex straight to slightly emarginate medially. Mentum lacking tooth. Mentum and submentum separated medially by transverse suture; such suture obliterated laterally in many specimens; state of suture laterally varied within some species. Ligula narrow; with or without distal dorsal setae. Paraglossa various in length, with setae on dorsal base and in many specimens with setae along mesal and dorso-mesal sides (setae may be difficult to discern in some species).

Pronotum with 2 lateral seta, 1 near middle and 1 towards posterior angle; lateral bead complete; apical and basal beads present at least laterally.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindfemur of most specimens with 2 long setae on posterior margin. Hindtarsus with segment I shorter to longer than II + III. Dorsum of all tarsi pubescent in most specimens.

Elytron. Scutellar stria unmodified or in some specimens long and joined distally with interval I; intervals flat to slightly convex; interval III and in some specimens interval VII with several dorsal setigerous punctures; interval VII with minute ocellate puncture at extreme apex and large prominent ocellate puncture slightly more proximally located.

Abdomen. Sternum VI of ♂ with 1 or 2 pairs of ambulatory setae.

Male genitalia. Median lobe lacking apical disc.

Female genitalia. Valvifer moderately sclerotized, varied in shape. Stylus with apical segment moderately to strongly elongate. Proctiger well sclerotized, distal portion free from tergum in many species.

Discussion. — The genus *Progonochaetus* is a well defined group possessing the apomorphic character states of: paraglossa with at least some setae on dorsal base and usually also elsewhere; pronotum with 2 lateral setae on each side; and apical segment of female stylus elongate.

The species of *Progonochaetus* comprise 2 groups based primarily on pronotal form. The first group is the nominate subgenus and includes those species in which the pronotum (Figs. 184, 186) is semirectangular in form, has a non-sinuate side, and non-projected posterior angle. The second group is the subgenus *Eudichirus* containing those species in which the pronotum (Fig. 187) is semicordate with the side sinuate before the outward projected posterior angle. The nominate subgenus contains those species included in *Progonochaetus* by Basilewsky (1950), all species formerly included by him in *Dichaetochilus* and *Oligoxemus*, and a single Oriental species formerly placed in the genus *Pseudognathaphanus*. The subgenus *Eudichirus* includes those species formerly included in *Eudichirus* and *Rasnodactylus* by Basilewsky (1950).

Progonochaetus was treated by Basilewsky (1950) as a monotypic genus containing only the species *xanthopus*. The paraglossa of *xanthopus* has long prominent seta along its mesal margins and on its dorsal base. Species of *Dichaetochilus*, *Oligoxemus*, *Rasnodactylus*, and *Eudichirus* were stated to have glabrous paraglossa and therefore to belong to different genera than *xanthopus*. However, dissection of specimens of these former 4 genera reveals that all their species have setae on the dorsal base and often also on the mesal margins of the paraglossa. These setae vary in number, length, thickness, and location according to the species being examined. The species *xanthopus* is merely a species in which the setae are especially long and numerous; its characters do not require that it be given separate generic status.

Basilewsky (1950) distinguished *Oligoxemus* from *Dichaetochilus* by possession of 2, rather than 1, setae at each outer distal angle of the clypeus. This single character is not sufficient to warrant separate generic or subgeneric status in view of the inter- and intra-specific variation shown by this character in *Anisodactylus*. Since the species of *Oligoxemus* and *Dichaetochilus* differ in no significant characters from *xanthopus*, both genera must be combined with *Progonochaetus*.

Basilewsky (1950) distinguished *Rasnodactylus* from other Anisodactyline genera due to its single species, *jeanneli*, possessing an unmodified male midtarsus (that is, not laterally expanded and not spongy pubescent beneath). However the state of the male midtarsus is not a reliable intergeneric character within Anisodactylina. For example, in the subspecies *Dicheirus dilatatus angulatus* the male midtarsus varies from unmodified to laterally expanded and spongy pubescent beneath (Noonan, 1968). The former genus *Eudichirus* was regarded as containing the species *ochropus* and *pseudochropus*. However, in both of these species the segments of male midtarsus are at most only very slightly expanded laterally and each bear only a relatively small patch of spongy pubescent vestiture. I have seen one male of *pseudochropus* in which the male midtarsus is completely unmodified. There is not sufficient

reason to keep separate the species of the former genera *Eudichirus* and *Rasnodactylus*.

The species *Dichaetochilus jeanneli* Basilewsky, 1946 and *Rasnodactylus jeanneli* Basilewsky, 1946 are now both members of the genus *Progonochaetus*. I here propose "basilewskyi" as a replacement name for the former species.

14 subgenus *Progonochaetus* G. Müller
(Figs. 184, 186)

Progonochaetus G. Müller, 1938: 245. [TYPE SPECIES: *Anisodactylus xanthopus* Dejean, 1829, by original designation].

Dichaetochilus Basilewsky, 1946 a: 7. [TYPE SPECIES: *Selenophorus aeruginosus* Dejean, 1829, by original designation. NEW SYNONYMY].

Oligoxemus Basilewsky, 1948: 66. [TYPE SPECIES: *Anisodactylus limbatus* Quedenfeldt, 1883, by original designation and monotypy. NEW SYNONYMY].

Description.

Thorax. Pronotum (Figs. 184, 186) semirectangular, somewhat transverse; side not sinuate; posterior angle not outward projected.

Legs. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath.

Discussion. — This subgenus contains 1 Oriental species and 38 Ethiopian ones. The single Oriental species, *laevistriatus* (Sturm), 1918, is found in India and Bruma. It was formerly placed in the genus *Pseudognathaphanus*. However in *laevistriatus*: the mentum and submentum are separated by a transverse suture which appears complete in some specimens, narrowed and vestigial laterally in others, and present medially but absent laterally in others; there are 2 pronotal lateral setae; the paraglossa has dorsal setae; and the apical segment of the female stylus is elongate.

The 38 Ethiopian species are found in Africa south of the Sahara and in Madagascar and are: *aeruginosis* (Dejean), 1829*; *angolanus* (Basilewsky), 1946; *approximatus* (Kolbe), 1897; *arnoldi* (Basilewsky), 1948; *atrofuscus* (Fairmaire), 1869*; *bamboutensis* (Basilewsky), 1948*; *basilewskyi*, *nomen novum* for *Dichaetochilus jeanneli* Basilewsky, 1946; *bicoloripes* (Burgeon), 1936; *brittoni* (Basilewsky), 1946; *caffer* (Boheman), 1848; *chevalieri* (Basilewsky), 1946*; *colmantii* (Burgeon), 1936; *cursorius* (Basilewsky), 1946; *decorsei* (Basilewsky), 1948*; *dilatatus* (Klug), 1853*; *discrepans* (Basilewsky), 1946; *emarginatus* (Dejean), 1829; *inchoatus* (Peringuery), 1908*; *incrassatus* (Boheman), 1848*; *kafakumbae* (Basilewsky), 1949*; *kapangae* (Burgeon), 1936; *laeticolor* (Chaudoir), 1876*; *limbatus* (Quedenfeldt), 1883; *longesulcatus* (Basilewsky), 1949*; *merus* (Basilewsky), 1949*; *moestus* (Chaudoir), 1878; *nigricrus* (Dejean), 1828*; *obtusus* (Basilewsky), 1946; *piceus* (Dejean), 1829*; *planicollis* (Putzeys), 1880; *prolixus* (Basilewsky), 1948*; *rudebecki* (Basilewsky), 1946*; *sakalava* (Jeannel), 1948*; *seyrigi* (Jeannel), 1948*; *straneoi* (Basilewsky), 1949*; *subcupreus* (Chaudoir), 1876; *vagans* (Dejean), 1831*; *xanthopus* (Dejean), 1829.

The 38 Ethiopian species can be distinguished by means of the generic and specific keys provided by Basilewsky (1950). The single Oriental species can be distinguished on the basis of its geographical distribution.

15 subgenus *Eudichirus* Jeannel NEW STATUS
(Fig. 187)

Eudichirus Jeannel, 1946: 158. [TYPE SPECIES: *Anisodactylus ochropus* Dejean, 1948, by original designation].

Rasnodactylus Basilewsky, 1946 b: 17. [TYPE SPECIES: *Rasnodactylus jeanneli* Basilewsky, 1946, by original designation. NEW SYNONYMY].

Description.

Thorax. Pronotum (Fig. 187) semicordate, with side sinuate before the pointed outward projected posterior angle.

Legs. Foretarsus of ♂ with some segments slightly expanded laterally and in some specimens spongy pubescent beneath. Midtarsus of ♂ unmodified in *jeanneli*, but in most specimens of other species with some segments slightly expanded laterally and spongy pubescent beneath.

Discussion. — The subgenus *Eudichirus* contains 3 very similar appearing named species which all occur in Africa: *jeanneli* (Basilewsky), 1946; *ochropus* (Dejean), 1829 ♀*; and *pseudochropus* (Kuntzen), 1919 ♀*. It is possible that the last 2 forms may be conspecific. The 3 species can be separated by using the generic and specific keys provided by Basilewsky (1950).

16 genus *Phanagnathus* Basilewsky

Phanagnathus Basilewsky, 1950: 35. [TYPE SPECIES: *Anisodactylus overlaeti* Burgeon, 1936, by monotypy and original designation].

Description. — Body length 9 to 10 mm. Body relatively stout.

Color. Body dark piceous to black.

Head. Labral apex moderately emarginate medially. Frons with fovea obsolescent, bearing weak clypeo-ocular prolongation; microsculpture obsolescent. Eye large and protruding. Gena narrow, width at narrowest point less than maximum width of first antennal segment. Mentum with moderately prominent tooth. Mentum and submentum completely fused. Submentum with 1 long seta on each side. Ligula narrow, slightly expanded laterally at apex. Paraglossa slightly longer than ligula.

Thorax. Pronotum transverse, constricted basally; lateral depression obsolescent; lateral bead complete; basal and apical beads present laterally; microsculpture obsolete in ♂, consisting of weak transverse mesh in ♀.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindfemur of most specimens with 2 long setae on posterior margin. Hindtarsus with segment I longer than II + III. Dorsum of all tarsi irregularly pubescent. Fore- and midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Scutellar stria short; intervals flat to slightly convex basally but more convex apically; interval III with several dorsal setigerous punctures apically; interval VII with distal ocellate puncture; subapical sinuation slight; microsculpture obsolescent in ♂, consisting of weak transverse mesh in ♂.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Tergum VIII of ♀ with apex obtusely angulate.

Male genitalia. Median lobe lacking apical disc.

Female genitalia. Valvifer slightly convex, moderately sclerotized, with several distal setae; distal mesal and lateral margins somewhat membranous.

Discussion. — This genus contains the single species *overlaeti* (Burgeon), 1936 which is found in the Belgian Congo.

17 genus *Pseudognathaphanus* Schauberger

Pseudognathaphanus Schauberger, 1932: 57. [TYPE SPECIES: *Harpalus punctilabris* MacLeay, 1825, by original designation].

Protognathus Basilewsky, 1950: 36. [TYPE SPECIES: *Anisodactylus zabroides* Alluaud, 1917, by original designation. NEW SYNONYMY].

Description. — Body length 9 to 15 mm. Body elongate, moderately convex.

Color. Body brown to black, no metallic tinge.

Head. Labral apex straight to slightly emarginate medially. Clypeal apex straight to moderately emarginate medially. Frontal fovea moderate, bearing prominent clypeo-ocular prolongation. Mentum lacking tooth. Mentum and submentum completely fused. Ligula narrow, not expanded laterally at apex. Paraglossa longer than ligula.

Thorax. Pronotum with lateral bead complete; apical and basal beads present at least laterally.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate to swollen basally. Hindfemur of most specimens with 2 long setae on posterior margin. Hindtarsus with first segment approximately 2.5 to 3 times as long as wide at apex, shorter than II + III. Segments II to IV of hindtarsus of both sexes and segments II to IV of fore- and midtarsus of ♀ with dense ventro-lateral cover of somewhat thickened setae. Fore- and midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals flat to slightly convex; specimens of *dekanus* with only 1 dorsal setigerous puncture, this puncture located near apical 1/5 of interval III, specimens of other species with several to many dorsal setigerous punctures located on various intervals; interval VII with minute ocellate puncture at extreme apex and large prominent ocellate puncture slightly more proximal.

Hind wing. Full and probably functional in all species examined.

Abdomen. Sternum VI with 1 or 2 pairs of ambulatory setae in ♂.

Male genitalia. Median lobe with or without apical disc.

Female genitalia. Valvifer various depending on species.

Jedlička (1957) treated *Pseudognathaphanus* (s. str.) as a subgenus of the genus *Kareya* Andrewes, 1919 because of the similar body shape of species of these groups. The description provided by Andrewes for the genus *Kareya* and the comments of Jedlicka (1957) make it apparent that the genus *Kareya* does not belong to the subtribe *Anisodactylina*. Therefore, the treatment proposed by Jedlicka (1957) is not accepted here.

The genus *Pseudognathaphanus* contains 6 species in the Oriental Region and 2 in Madagascar. The latter 2 species previously constituted the genus *Protognathus*, but no constant morphological characters warrant separate generic status for *Pseudognathaphanus* and *Protognathus*. And the species of these 2 groups are characterized by the apomorphic feature of segments II to IV of the hindtarsus of both sexes and segments II to IV of fore- and midtarsus of females with a dense ventro-lateral cover of somewhat thickened setae.

The 6 Oriental Region species of *Pseudognathaphanus* are found in India, Ceylon, Burma, and Indochina except for the widespread species *punctilabris* which also occurs in China, Formosa, and Philippine Islands, Java, and Sumatra. These species are: *dekanus* Andrewes, 1933; *exaratus* (Bates), 1892; *festivus* (Andrewes), 1921 ♂*; *punctilabris* (MacLeay), 1825; *rufitactor* (Bates), 1892*; *rusticus* (Andrewes), 1920. The 2 species on Madagascar are:

perrieri (Jeannel), 1948*; and *zabrooides* (Alluaud), 1917. The species of the Oriental Region may be identified by the key in Jedlicka (1957). The 2 species found on Madagascar may be distinguished by the keys in Basilewsky (1950).

18 genus *Chydaeus* Chaudoir
(Fig. 172)

Chydaeus Chaudoir, 1854: 343. [TYPE SPECIES: *Chydaeus obscurus* Chaudoir, 1854, by monotypy].

Acrogeniodon Tschitscherine, 1897: 65. [TYPE SPECIES: *Acrogeniodon bedeli* Tschitscherine, 1897, by monotypy].

Hayekius Habu, 1955: 35. [TYPE SPECIES: *Ophonus constrictus* Bates, 1833, by monotypy].

Description. — Body length approximately 9 to 14 mm. Body narrow, but in some specimens appearing stout due to broad elytra.

Color. Body dark piceous to black.

Head. Labral apex strongly emarginate medially. Frontal fovea obsolescent to moderately prominent and punctiform or somewhat linear, with or without clypeo-ocular prolongation. Mentum with very prominent, long tooth (Fig. 172). Mentum and submentum completely fused. Ligula narrow or moderately expanded at apex. Paraglossa slightly longer than ligula and well removed distally from it.

Thorax. Pronotum relatively small, somewhat cordate; lateral bead complete; basal bead complete in most specimens, but obsolescent medially in some specimens. Apical bead present laterally.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindfemur of most specimens with 2 long setae on posterior margin. Hindtarsus with segment I slightly shorter to slightly longer than II + III. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Scutellar stria with length varied within individual species, in many specimens distal portion of stria I captured and base of stria I left as apparent false scutellar stria (see discussion); intervals flat to convex, no setigerous punctures; interval VII with distal ocellate puncture.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Tergum VIII of ♀ with rounded apex.

Male genitalia. Median lobe lacking apical disc.

Female genitalia. Valvifer slightly convex, moderately sclerotized, with several distal setae; distal mesal margin somewhat membranous and without discrete boundary. Proctiger modified into moderately sclerotized elongate plate on each side of anal orifice and with or without setae.

Discussion. — Tschitscherine (1897), who apparently never saw identified specimens of *Chydaeus*, described the monobasic *Acrogeniodon*. Andrewes (1919) treated it as congeneric with *Chydaeus*, and subsequent authors have accepted this treatment.

Habu (1955) and Tanaka (1958) accorded the species *constrictus* separate generic status in the monotypic genus *Hayekius*. Habu (1973) treated *Hayekius* as congeneric with *Chydaeus* but did not give reasons for this treatment. Habu (1955) and Tanaka (1958) originally felt *Hayekius* warranted separate generic status because its sole species, *constrictus*, was stated to have the scutellar stria originating on the first elytral interval and the metepisternum not longer than wide. But the holotype of *constrictus* has an unmodified scutellar

stria arising from an ocellate puncture at the base of stria II; and considerable variation of the scutellar stria occurs in *constrictus*, *bakeri* and probably other species of *Chydaeus*. The scutellar stria in specimens of *constrictus* and *bakeri* can be: (1) unmodified; (2) elongate, curved distally towards stria I; (3) elongate, joining stria I distally; (4) elongate, completely capturing the distal portion of stria I, with basal portion of stria I nearly reaching point of juncture; (5) elongate, completely capturing the distal portion of stria I, basal portion of stria I short and appearing on first glance to be the scutellar stria. The length of the metepisternum varies depending on whether the hind wings are functional or vestigial.

Schauberger (1934) provided a key to the species known at that time, and Habu (1973) provided a fine key to the species found in Japan. Additional species have been described since Schauberg's revision, and *Chydaeus* is in need of revision.

Species of the genus are concentrated in southern China, northern India, Tibet, and Sikkim but some occur as far towards Australia as New Guinea. The 20 named species are: *andrewesi* Schauberger, 1932; *bakeri* Andrewes, 1926; *bedeli* (Tschitscherine), 1897; *constrictus* (Bates), 1883; *formosanus* Tanaka, 1958*; *gestroi* Andrewes, 1929; *hinnus* Darlington, 1971*; *javanicus* Schauberger, 1932; *qedlickai* Schauberger, 1934*; *kirishimanus* Habu, 1973*; *miwai* Jedlicka, 1946*; *obscurus* Chaudoir, 1854; *obtusicollis* Schauberger, 1932; *papua* Darlington, 1968; *planicollis* Andrewes, 1931; *rufipes* Jedlicka, 1940*; *schaubergeri* Jedlicka, 1931; *shibatai* Habu, 1973*; *shikokuensis* Habu, 1973*; and *yunnanus* Jedlicka, 1940*. Darlington (1968) mentioned that many of the species are restricted to mountainous areas.

19 genus *Harpalomimetes* Schauberger

Harpalomimetes Schauberger, 1933: 133. [TYPE SPECIES: *Anisodactylus sjostedti* Andrewes, 1926, by original designation].

Description. — Body slender, dorsal microsculpture obsolescent or absent, dorsum covered with fine non-setigerous punctures.

Color. Body black. Elytron iridescent.

Head. Rather large with broad neck. Labral apex moderately emarginate medially. Clypeal apex moderately emarginate medially. Frontal fovea punctiform, with fine but discernible clypeo-ocular prolongation. Mentum without tooth. Mentum and submentum completely fused. Ligula narrow, slightly expanded laterally at apex. Paraglossa slightly longer than ligula, separated distally from it.

Thorax. Pronotum suborbiculate; lateral bead complete; apical and basal beads present at least laterally; sides and lateral portions of base and apex with small dense non-setigerous punctures.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur lanceolate. Hindtarsus with segment I shorter than II + III. Fore- and midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals slightly to moderately convex and iridescent, more so in ♂; interval III with dorsal setigerous puncture near apical 1/3; interval VII with apical ocellate puncture; microsculpture absent.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae.

Male genitalia. Median lobe with very small apical disc.

Female genitalia. Valvifer moderately sclerotized, subtriangular in shape, with several distal setae.

Discussion. — This genus contains the 2 species: *sjostedti* (Andrewes), 1926 found in Sumatra and the Philippines; and *andrewesi* Schauberger, 1933 found in Indochina and

Japan. I have not examined specimens of *andrewesi*. Tanaka (1958) redescribed that latter species, and I have relied on this redescription in preparing the generic description.

20 genus *Rhysopus* Andrewes

Rhysopus Andrewes, 1929: 358. [TYPE SPECIES: *Rhysopus klynstrai* Andrewes, 1929, by monotypy].

Description. — Body length 11 to 12 mm.

Color. Body black; shiny and faintly iridescent due to reduced microsculpture.

Head. Large with broad neck. Labral apex strongly emarginate medially. Clypeal apex moderately emarginate medially. Frontoclypeal suture extremely deep, extended laterally to region of frontal fovea then postero-laterally toward eye as very deep clypeo-ocular prolongation. Frontal fovea obliterated by the very deep frontoclypeal suture. Mentum completely fused to submentum and lacking tooth or setae. Ligula strongly expanded laterally at apex. Paraglossa slightly longer than ligula, separated distally from it.

Thorax. Pronotum widest just before middle, sides thence convergent towards base; posterior angle broadly rounded; side and lateral portion of base with coarse non-setigerous punctures and lateral portion of apex with smaller non-setigerous punctures; lateral bead complete; apical and basal beads present laterally and in most specimens also medially.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur trifid. Hindfemur with 2 long setae on posterior margin. Hindtarsus with segment I = to II + III in most specimens. Fore- and midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals convex and with numerous small non-setigerous punctures; interval III with dorsal setigerous puncture about 1/3 from apex; interval VII with apical ocellate puncture; stria deep and wide; subapical sinuation moderate; microsculpture of extremely fine transverse lines.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Tergum VIII of ♀ with rounded apex.

Male genitalia. Median lobe without apical disc.

Female genitalia. Valvifer moderately sclerotized, apical portion becoming narrower and blade like distally and with several distal setae.

Discussion. — *Rhysopus* includes only the single species *klynstrai* Andrewes, 1929 found in Java, Sumatra, and the Tonkin area of Indochina. In describing this genus, Andrewes emphasized the male fore- and midtarsi which he reported to have on the underside of the expanded segments "12 to 15 fine longitudinal ridges, and twice as many scales, transversely placed between each two adjacent ridges". Actually the ridges are merely the basal portions of the setae which distally form the spongy pubescence found in Anisodactylines, and the male tarsi thus are not different from those found in other Anisodactylines. However *klynstrai* warrants separate generic status due to the extremely deep frontoclypeal suture and the elytral microsculpture of extremely fine transverse lines.

21 genus *Xestonotus* LeConte

(Figs. 173, 212, 213, 227)

Xestonotus LeConte, 1853: 383. [TYPE SPECIES: *Selenophorus lugubris* Dejean, 1829, by monotypy].

Description. — Body length 9.2 to 11.0 mm. Body relatively slender with large head and small eyes.

Color. Body rather dull black.

Head. Frontal fovea punctiform, small. Mentum without tooth. Mentum and submentum completely fused. Ligula (Fig. 173) not expanded laterally at apex; moderately to strongly laterally expanded subapically. Paraglossa (Fig. 173) subequal to or slightly longer than ligula; apex obtuse.

Thorax. Pronotum broad with all angles rounded; lateral bead fine but complete; apical and basal beads present, flattened and obsolete medially in most specimens; microsculpture of slightly transverse isodiametric mesh, more prominent in ♀. Prosternum sparsely pubescent. Proepisternum, mesepisternum, mesepimeron, metepisternum, metepimeron glabrous. Mesosternum pubescent. Metasternum sparsely pubescent near midcoxa and in some specimens near midline.

Legs. Foretibia with distal portion slightly expanded laterally; apex emarginate, outer angle of emargination rounded; apical spur lanceolate. Hindtarsus with segment I = to II + III in most specimens. Dorsum of all tarsi sparsely pubescent. Foretarsus of ♂ with segments I to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Interval III of most specimens with dorsal setigerous puncture adjacent to stria II on apical 1/3; microsculpture of slightly irregular and slightly granulate isodiametric mesh, more prominent in ♀.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Tergum VIII of ♀ with apex rounded.

Male genitalia. Median lobe (Figs. 212, 213) strongly asymmetrical, swollen medially; apex bent ventrad; right latero-ventral margin with small serrations. Internal sac in repose with prominent spine inserted on scaly field protruded through ostium; everted sac with 2 prominent spines, one apical and with small scaly field at base, other basal (one which protrudes from ostium when sac in repose) and with scaly field extended distally from it.

Female genitalia. Valvifer (Fig. 227) flattened, moderately sclerotized, with varied number of distal setae.

Discussion. — This genus contains only the species *lugubris* (Dejean), 1829 found in southeastern Canada and the eastern United States. Past workers have treated *Xestonotus* as a separate genus or included it in *Anisodactylus*. Although Lindroth (1968) treated it as a subgenus of *Anisodactylus* because he found no external characters to warrant generic separation, he did so reluctantly because of the very different and highly asymmetrical median lobe of *lugubris*. However the ligula of *lugubris* differs from that of all species of *Anisodactylus*, and *lugubris* is accorded separate generic status.

22-31 genus *Anisodactylus* Dejean

Anisodactylus Dejean, 1829: 132. [TYPE SPECIES: *Carabus binotatus* Fabricius, 1787, designated by Westwood (1838)].

Description. — Body length 7.0 to 19 mm. Body stout and *Amara*-like to cylindrical and convex.

Color. Various.

Head. Clypeus with 1 to several setigerous punctures at each outer angle. Frons with fovea various but in most specimens with clypeo-ocular prolongation; microsculpture in most species of isodiametric mesh, obsolete medially in some species, of granulate isodiametric mesh or of punctures in a few species. Mentum without tooth or with small tooth. Mentum and submentum completely fused. Ligula strongly expanded laterally at apex, or only moderately expanded in specimens of *californicus*, *furvus*, and *kirbyi*. Paraglossa membranous,

slightly longer than ligula.

Thorax. Pronotum with lateral, apical, and basal beads present; microsculpture of isodiametric mesh, or granulate isodiametric mesh, of punctures, or obsolete.

Elytron. Outer intervals, base, and apex pubescent in some species; inner intervals not densely and regularly pubescent.

Abdomen. Sternum VI of ♂ with 1 or 2 pairs of ambulatory setae.

Male genitalia. Median lobe arcuate except in subgenus *Pseudhexatrichus*; with or without apical disc. Internal sac with or without armature.

Female genitalia. Valvifer various, constant in shape for species of most subgenera.

Discussion. — This is the largest genus in the subtribe and contains 10 subgenera and 54 species. The genus is found in North America, Europe to tropical Asia, areas adjacent to the Mediterranean, northern Africa, Japan, Korea, India, Burma, and Indochina.

Authors have had differing opinions as to the exact composition of the genus. These opinions are reviewed under the 10 subgenera recognized here.

Information on the identification of specimens is also presented in the discussion section for each subgenus.

I have not determined the proper subgeneric placement of 7 species of which I have not seen examples and of which I can not gain sufficient information from the literature. These 7 species are: *abaculus* Bates, 1889, described from Liberia; *amplicollis* Gerstaecker, 1867, described from east Africa; *mandschuricus* Jedlicka, 1924, described from Manchuria, China; *metallescens* Putzeys, 1880, described from Angola; *obscuripes* LaFerté, 1853, described from Africa; *obtusicollis* Putzeys, 1880, described from Angola; and *schaubergi* Jedlicka, 1932, described from Yunnan, China. The 5 species from Africa may belong to genera other than *Anisodactylus*.

22 subgenus *Anisodactylus* Dejean
(Figs. 198, 217, 218)

Anisodactylus Dejean, 1829: 132. [TYPE SPECIES: *Carabus binotatus* Fabricius, 1787, designated by Westwood (1838)].

Cephalogyna Casey, 1918: 414. [TYPE SPECIES: *Anisodactylus lodingi* Schaeffer, 1911, by monotypy].

Description. — Body length approximately 7 to 19 mm. Body convex, with pronotum small and elytra elongate and subparallel.

Color. Body color unmetallic piceous to black. Frons except for occasional specimens in some species, with double more or less confluent rufous spot medially.

Head. Labral apex straight to strongly emarginate medially. Clypeus with apex straight to moderately emarginate medially; species of the Old World with 1 setigerous puncture at each outer distal angle; species of the New World with 1 to several (number varied within many species) setigerous punctures at each outer distal angle. Frontal fovea various, in most specimens with more or less evident clypeo-ocular prolongation, also in many specimens with medially directed prolongation producing a somewhat Y shaped fovea. Mentum without a tooth or with small tooth in some specimens of various North American species. Paraglossa slightly longer than ligula.

Thorax. Shape and form of pronotum various. Prosternum of most specimens pubescent at sides; glabrous or pubescent medially.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur dilated near base, varied within several species from evenly dilated and non angulate to strongly angulate or even subtrifid (as in most specimens of *similis*), clearly trifid in *carbonarius*, *tricuspidatus*,

and *karennius*. Hindfemur with 2 long setae, or in specimens of *carbonarius*, *similis*, *signatus*, and *binotatus* with 2 to 5 such setae. Hindtarsus with segment I = to or longer than II + III in all species but *signatus*, *tricuspidatus*, *nemorivagus* and *karennius*. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with apex of segment I in some specimens and all of segments II to IV in all specimens laterally expanded and spongy pubescent beneath.

Elytron. Humerus rounded to angulate depending on species; outer intervals, base, and apex pubescent in some species; intervals flat to convex; interval III with single dorsal setigerous puncture, such puncture lacking in *signatus*, and *tricuspidatus* with 1 to 2 such punctures; intervals II and V of some specimens with 1 or more distal setigerous punctures; interval VII with distal ocellate puncture and in some specimens with 1 or more distal setigerous punctures; intervals of some specimens covered with non-setigerous punctures.

Hind wing. Full and apparently functional in all species except *agricola*.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae in most species. Apex of tergum VIII of ♀ broadly rounded (Fig. 198).

Male genitalia. Median lobe with apex symmetrical and lacking disc; shaft twisted in *binotatus*; membranous portion of dorsum various in size and extension towards basal bulb, nearly reaching basal bulb in several species, in *similis* reaching basal bulb and occupying most of dorsum distal to it, divided into 2 parts in *binotatus*. Internal sac with or without armature.

Female genitalia. Valvifer strongly sclerotized; distal portion triangular in shape and with setae of various numbers and sizes (Figs. 217, 218).

Discussion. — This is the most widespread subgenus of the subtribe and is represented in temperate North America, Europe to China, Japan, Korea, Burma, and Africa north of the Sahara Desert. It was formerly thought to also be present in tropical Africa, but Basilewsky (1950) demonstrated that the species there belong to a different genera.

The North American forms are well understood since Lindroth (1968) completed an excellent revision and provided a key to them. Puel (1931) provided a usable key to species of the Palearctic region, Jeannel (1942) keyed out those of France, and Tanaka (1958) provided good keys to those of Japan and in part to those of Korea and China. And Habu (1973) provided fine keys to the species of Japan.

The only species not treated in one of the above works are *karennius* (Bates), 1892 and *pueli* Schaeffer, 1933. The species *karennius* is found in India, Burma, and Indochina. Csiki (1932) listed *hauseri* Schaeffer as being conspecific with *karennius*. However, Puel (1931) cited *hauseri* as having a simple foretibial apical spur while the foretibial apical spur in the 7 specimens I have seen of *karennius* are trifid. The only other Palearctic species possessing a trifid foretibial apical spur is *tricuspidatus*. The species *karennius* and *tricuspidatus* are distinguished from each other by elytron of *karennius* glabrous except for a dorsal puncture on interval III and an apical ocellate puncture on interval VII, and elytral intervals of *tricuspidatus* densely covered with non-setigerous punctures. The species *pueli* is recorded from Albania to Turkey; I have seen only 1 female specimen of it and can not provide information on distinguishing this form from other species.

I have seen males and females of all 13 North American species. These species are: *agricola* (Say), 1823; *binotatus* (Fabricius), 1787 (introduced from Eurasia); *californicus* Dejean, 1829; *carbonarius* (Say), 1823; *consobrinus* LeConte, 1851; *furus* LeConte, 1863; *harrisi* LeConte, 1863; *loeddingi* Schaeffer, 1911; *kirbyi* Lindroth, 1953; *melanopus* Halde- man, 1843; *nigerrimus* (Dejean), 1831; *nigrita* Dejean, 1829; and *similis* LeConte, 1851.

Casey (1918) proposed a separate genus, *Cephalogyna*, for the species *loeddingi*. Lindroth (1968) quite correctly regarded *Cephalogyna* as congeneric with the subgenus *Anisodactylus*.

While *loeddingi* is the largest species in the subgenus, and in fact in the genus, it has the type of female valvifer and female abdominal tergum VIII diagnostic for the subgenus *Anisodactylus*.

The species *carbonarius* was formerly treated as a member of the subgenus *Gynandrotarsus* because of its trifid foretibial apical spur. However, this character is not diagnostic as formerly believed. The Old World species *tricuspidatus* and *karennius* also have trifid foretibial spurs, and several North American species have swellings or are slightly angulate at each side of their spurs. Lindroth (1968) pointed out that *carbonarius* has the general habitus (more slender than that of *Gynandrotarsus*) of species of the subgenus *Anisodactylus* and has pubescence medially on the prosternum. "True" *Gynandrotarsus* have the prosternum glabrous medially, possess the type of female valvifer described for that subgenus, and have the apex of the female abdominal tergum VIII angulate. Instead *carbonarius* has the type of female valvifer and the apically more rounded female abdominal tergum VIII found in all members of the subgenus *Anisodactylus*, and I am here transferring *carbonarius* to this taxon.

The 12 species found in the Old World are: *antoinei* Puel, 1931*; *atricornis* (Stephens), 1835*; *binotatus* (Fabricius), 1787; *hauseri* Schauberger, 1931*; *hispanus* Puel, 1931 ♀*; *karennius* (Bates), 1892; *nemorivagus* Duftschmidt, 1812; *nigricornis* (Stephens), 1835*; *propinquus* Ballion, 1870*; *shibatai* Habu, 1969*; *signatus* (Panzer), 1797; and *tricuspidatus* Morawitz, 1863.

The species *sadoensis* Schauberger, 1931 and *punctatipennis* Morawitz, 1862 formerly considered members of this subgenus have been removed to a new subgenus, *Pseudanisodactylus*, for reasons discussed under that taxon.

Jeannel (1942) treated the subgenus *Pseudodichirus* with its single species *intermedius* Dejean, 1829 as congeneric with the subgenus *Anisodactylus*. For reasons discussed under the subgenus *Pseudodichirus*, I have revalidated this subgenus and transferred *intermedius* back to it.

23 *Pseudanisodactylus* NEW SUBGENUS

(Fig. 221)

TYPE SPECIES: *Anisodactylus punctatipennis* Morawitz, 1862, here designated.

Description. — Body length 9.5 to 13.5 mm. Body form as in nominate subgenus; entire dorsum densely covered with small non-setigerous punctures.

Color. Body dark piceous to black. Head with frons bearing median rufous spot.

Head. Labral apex moderately to strongly emarginate medially. Clypeal apex straight to moderately emarginate medially. Frontal fovea Y shaped, one arm forming clypeo-ocular prolongation, other arm directed medially. Paraglossa slightly longer than ligula.

Thorax. Pronotum cordiform. Prosternum densely pubescent. Proepisternum pubescent anteriorly, remainder without pubescence but covered with non-setigerous punctures. Proepimeron, mesepisternum, mesepimeron, metepisternum, metepimeron covered with non-setigerous punctures but lacking pubescence in most specimens. Meso- and metasternum pubescent.

Legs. Foretibia with distal portion moderately expanded laterally; apex weakly emarginate in ♂, more prominently emarginate in ♀; apical spur obtusely dilated near middle. Hindtarsus relatively slender; segment I = to II + III in most specimens. Dorsum of all tarsi densely pubescent.

Elytron. Apex and base of intervals I to VII, all of intervals VIII to X pubescent; interval III without dorsal setigerous puncture.

Abdomen. Sternum VI with 1 pair of ambulatory setae in ♂. Abdominal tergum VIII of ♀ as in nominate subgenus (Fig. 198).

Male genitalia. Median lobe lacking apical disc.

Female genitalia. Valvifer (Fig. 221) moderately sclerotized, slightly convex, lobed; with several distal setae of various numbers, sizes and arrangements.

Discussion. — This new subgenus contains the species *punctatipennis* Morawitz, 1862 found in Japan, Korea, and China, and the species *sadoensis* Schauberger, 1931 found in Japan. These 2 species were formerly placed in the subgenus *Anisodactylus* but differ from all species of that subgenus by valvifer lobed, nontriangular. The species *punctatipennis* and *sadoensis* are distinguished from other Asian species of *Anisodactylus* by the key in Tanaka (1958).

Derivation of name. — The name “*Pseudanisodactylus*” refers to the close external resemblance of included species to those of the subgenus *Anisodactylus*.

24 subgenus *Pseudhexatrichus* NEW SUBGENUS (Figs. 191, 214, 215, 219)

Pseudhexatrichus Puel, 1931: 61. [NOMEN NUDUM (see discussion) TYPE SPECIES: *Anisodactylus dejearni* Buquet, 1840, here designated].

Description. — Body length 9.5 to 12.5 mm. Body form as in nominate subgenus.

Color. Dorsum bicolored; head rufotestaceous; pronotum bluish black; elytron rufotestaceous basally, bluish black medially and apically.

Head. Labral apex slightly to moderately emarginate medially. Clypeal apex straight to slightly emarginate medially. Frontal fovea with clypeo-ocular impression, in some specimens also with medially directed linear impression. Mentum without or with vestigial tooth. Paraglossa slightly longer than ligula.

Thorax. Pronotum constricted basally; pubescent near anterior angle. Prosternum pubescent except for median glabrous area. Proepisternum pubescent anteriorly, glabrous elsewhere. Remainder of venter pubescent.

Legs. Hindfemur with 2 long setae on posterior margin. Foretibia with inner basal margin broadly emarginate in ♂ (Fig. 191), unmodified in ♀; apical spur dilated medially but not clearly angulate; apex with brief emargination near outer angle. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath. Hindtarsus relatively slender; segment I = to or slightly shorter than II + III.

Elytron. Interval III of most specimens with 2 dorsal setigerous punctures on apical 1/3 (a few specimens with 1 or 3 such punctures); interval VII with 2 to 6 apical setigerous punctures.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae. Apex of tergum VIII of ♀ obtusely rounded.

Male genitalia. Median lobe (Figs. 214, 215) with shaft only very slightly arcuate and with distal portion asymmetric and bent to right.

Female genitalia. Valvifer (Fig. 219) as in nominate subgenus. Stylus with apical segment slightly compressed latero-medially.

Discussion. — This subgenus contains 2 species: *heros* (Fabricius), 1801 from Portugal, Spain, Sardinia, Algeria, and Morocco; and *dejearni* Buquet, 1840 from Algeria, Tunisia, and Sardinia. The 2 species are identified in the key provided by Puel (1931).

In his key to the Palearctic species of *Anisodactylus*, Puel (1931) assigned the subgeneric name “*Pseudhexatrichus*” to these species. However he did not designate a type species for the subgenus, and the subgeneric name proposed by him must therefore be regarded as a

nomen nudum according to the provisions of article 13b of the International Code of Zoological Nomenclature. For reasons outlined below I feel *heros* and *dejeani* should be ranked in a separate subgenus, and validate Puel's name since it has been accepted by other workers such as Csiki (1932).

The species *heros* and *dejeani* are closely related to those of the nominate subgenus as evidenced by the identical type of *valvifer* but warrant separate subgeneric status due to: bicolored rufotestaceous and bluish black dorsum; less prominently emarginate foretibial apex; broadly emarginate inner basal margin of the male foretibia; obtusely rounded apex of the female abdominal tergum VIII; and median lobe with shaft only very slightly arcuate and asymmetrical distally.

25 subgenus *Hexatrichus* Tschitscherine

(Figs. 192, 199, 222)

Hexatrichus Tschitscherine, 1898: 138. [TYPE SPECIES: *Harpalus poeciloides* Stephens, 1828, designated by Jeannel (1942)].

Description. — Body length 10 to 12 mm. Body form as in nominate subgenus.

Color. Various within species, dorsum of most specimens with metallic tinge.

Head. Labral apex slightly to moderately emarginate medially. Clypeus with 2 setae at each outer distal angle; apex straight to slightly emarginate medially. Frontal fovea with prominent clypeo-ocular prolongation. Mentum without or with slight tooth. Venter of head sparsely and irregularly pubescent. Paraglossa slightly longer than ligula.

Thorax. Pronotum pubescent near margins. Prosternum pubescent. Proepisternum pubescent anteriorly, glabrous posteriorly. Remainder of venter pubescent.

Legs. Forefemur of ♂ with obtuse tooth on apical 1/3 of posterior margin, tooth absent or weak in some specimens of *poeciloides*. Foretibia of ♂ (Fig. 192) with inner basal margin strongly and abruptly emarginate; unmodified in ♀; distal portion in both sexes moderately expanded laterally; apical spur trifid. Fore- and midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Hindfemur with numerous setae of various lengths along posterior margin. Hindtarsus relatively slender; segment I of most specimens equal to or longer than II + III. Dorsum of all tarsi sparsely pubescent.

Elytron. Rather flat in appearance, not prominently curved ventrad near apex; intervals VIII, IX, and X, or only IX and X pubescent basally and medially and in most specimens all intervals pubescent apically; interval III with 1 dorsal setigerous puncture near apical 1/3; interval III in most specimens and intervals V and VII in some specimens with series of apical setigerous punctures (larger than other punctures bearing pubescence).

Abdomen. Sternum I of some specimens, sterna II to IV of all specimens and proximal portion of sternum VI of some specimens pubescent (pubescence most prominent medially); sternum VI of ♂ with 2 pairs of ambulatory setae. Apex of ♀ tergum VIII (Fig. 199); more angulate than in nominate subgenus.

Male genitalia. Median lobe short and relatively stout; lacking apical disc; ventral and lateral surfaces with prominent longitudinal striae.

Female genitalia. Valvifer (Fig. 222) moderately sclerotized; flattened, similar in shape to that of nominate subgenus except broader and with blunter apex; distal portion with setae of various numbers and sizes; proximal lateral margin with membranous area.

Discussion. — This subgenus contains 3 species: *virens* Dejean, 1829, southwestern Europe and northern Africa; *poeciloides* (Stephens), 1828, England, central Europe to Norway and southern Russia, Balkan peninsula, and around northern border of Mediterranean to Persia;

and *mandschuricus* Jedlicka, 1942* described from "Mandschuk" (possibly this refers to the Manchuria area of China). The former 2 species can be identified by keys in Puel (1931) and Jeannel (1942).

26 subgenus *Pseudodichirus* Lutshnik
(Fig. 220)

Pseudodichirus Lutshnik, 1921: 3. [TYPE SPECIES: *Anisodactylus intermedius* Dejean, 1829, by monotypy].

Description. — Body length 12 to 14 mm. Body form as in nominate subgenus.

Color. Body piceous to black.

Head. Labral apex strongly emarginate medially. Clypeal apex slightly to moderately emarginate medially. Frons with fovea bearing clypeo-ocular prolongation and medially directed linear depression, producing a somewhat Y shaped fovea; microsculpture of isodiametric mesh. Mentum with tooth. Paraglossa slightly longer than ligula.

Thorax. Pronotum with sides strongly convergent basally. Prosternum pubescent except for median glabrous area.

Legs. Foretibial apical spur trifid. Hindtarsus relatively stout; segment I shorter than II + III. Dorsum of all tarsi with very sparse and irregular pubescence. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Interval III with dorsal setigerous puncture adjoining stria II towards apical 1/3; intervals III, V, VII with 1 to several apical setigerous punctures.

Hind wing. Full and apparently functional.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Apex of ♀ tergum VIII as in nominate subgenus.

Male genitalia. Median lobe lacking apical disc; membranous area of dorsum relatively long.

Female genitalia. Valvifer (Fig. 220) moderately sclerotized; subtriangular and with truncate apex; without setae; lateral margin somewhat membranous and indistinctly defined proximally.

Discussion. — This subgenus contains only the species *intermedius* which occurs all around the Mediterranean. Jeannel (1942) treated this subgenus as congeneric with the subgenus *Anisodactylus*. However *intermedius* warrants separate subgeneric status due to: female valvifer lacking setae and different in form (Fig. 220) from that constantly found in members of nominal subgenus (Figs. 217, 218); and mentum bearing moderate sized tooth (mentum of species in the nominate subgenus has at most a very small tooth in occasional specimens of some species). As discussed in the section on phylogeny, *intermedius* is the sister group of the subgenus *Gynandrotarsus*.

27 subgenus *Gynandrotarsus* LaFerté

Gynandrotarsus LaFerté, 1841a: 202. [TYPE SPECIES: *Gynandrotarsus harpaloides* LaFerté by monotypy].

Triplectrus LeConte, 1848: 381. [TYPE SPECIES: *Harpalus rusticus* Say, designated by Lindroth (1968)].

Description. — Body length 7.2 to 15.0 mm. Body rather stout and *Amara*-like.

Color. Body predominantly rufopiceous to black, except with slight greenish tinge to dorsum in many specimens of *opaculus* and with prominent greenish tinge to dorsum in all

specimens of *harpaloides*.

Head. Frontal fovea in some species bearing clypeo-ocular prolongation. Mentum unarmed or in most species with slight median tooth.

Thorax. Pronotum broad and wider than elytra measured across humeri in many species; side more or less rounded, not sinuate; lateral groove various; lateral bead, except in *hapolomus*, evident along entire length from base to apex though in many species fine near apex; apical and basal beads distinct laterally, but obsolescent medially in most specimens. Prosternum glabrous medially, elsewhere with very fine short pubescence. Proepisternum glabrous except for short fine pubescence near anterior margin. Mesosternum of most specimens with fine short pubescence, glabrous in some specimens. Metasternum generally glabrous except for patch of fine short pubescence adjacent to midcoxa. Mesepisternum, mesepimeron, metepisternum, metepimeron glabrous.

Legs. Foretibia somewhat triangular due to strong lateral expansion of distal portion; anterior face with single row of 5 to 9 setigerous punctures extended proximally from apex; apex weakly emarginate with outer angle somewhat rounded and reduced (Fig. 45); apical spur strongly trifid (Fig. 45). Hindfemur with 2 long setae on posterior margin. Hindtarsus with segment I as long or longer than II + III. Last segment of all tarsi with 3 to 5 pairs of ventral setae. Fore- and midtarsi of ♂ with apex of segment I of most specimens and all of segments II to IV of all specimens laterally expanded and spongy pubescent beneath.

Elytron. Humerus with or without tooth; intervals flat to convex, glabrous in most specimens; intervals III (only V and VII in some *harpaloides*), V, and VII with apical series of setigerous punctures, arrangement and number of such punctures various within individual species.

Hind wing. Fully developed and apparently functional in all species.

Abdomen. Tergum VIII of ♂ with strongly angulate apex (Fig. 60).

Male genitalia. Median lobe symmetrical, except left side of apical disc slightly elevated in *ovularis*; surface with predominantly longitudinal striae which vary in arrangement and prominence within individual species, transverse stria also present in some specimens; with or without apical disc. Internal sac with small scales and scale-like spines, larger sclerotized structures present in *texanus*, *harpaloides*, *dulcicollis*, and *opaculus*; in repose appearing as simple tubular sac following shape of median lobe, except irregularly coiled inside median lobe in *dulcicollis*.

Female genitalia. Valvifer shaped as in Fig. 130, heavily sclerotized, glabrous, convex in ventral view except for concave distal area; convex distal portion in many specimens separated from proximal convex area by slight ridge, presence of ridge varied with individual species.

Discussion. — *Gynandrotarsus* was originally proposed as a separate genus by LaFerte (1841a). Subsequent authors treated it as a separate genus, as a subgenus, or as a species group of *Anisodactylus*. *Triplectrus* was proposed by LeConte (1848) as a subgenus of *Anisodactylus*, and most workers have so regarded it. Casey (1914) combined *Gynandrotarsus* and *Triplectrus*. Ball (1960a: 1963) accepted this union but pointed out that *Gynandrotarsus* has priority and treated the taxon as a subgenus of *Anisodactylus*.

Casey (1914) provided a key to the forms he recognized as valid and also proposed 5 new species. In 1924 Casey provided descriptions for 11 new species, but no key accompanied these descriptions. All of the species he proposed in 1924 and all but one of those proposed in 1914 are here regarded as conspecific with previously described species. Lindroth (1968) provided a fine revision of the northern species of *Gynandrotarsus*. However, he felt that there were additional southern forms and that a complete revision of the subgenus was warranted (personal communication). Such a revision has been done in this paper.

The union of *Triplectrus* and *Gynandrotarsus* and the treatment of this group as a subgenus of *Anisodactylus* seem well justified to me. The species *harpaloides* and *opaculus* ("true" *Gynandrotarsus*) are characterized by the foretarsus of the female having the first segment laterally expanded. However, as pointed out by Lindroth (1968) this expansion is also slightly developed in *dulcicollis* and *texanus* ("true" *Triplectrus*), and these latter 2 species agree with the former 2 in having a clypeo-ocular prolongation on the frontal fovea of the head. The above 4 species and other species of the subgenus *Gynandrotarsus* share: trifid foretibial apical spur; short apical row of setigerous punctures on elytral intervals V and VII (also in most specimens on III); and type of female genitalia described above. Although well defined by the above combination of characters, *Gynandrotarsus* possesses no phenetically striking characters suggesting separate generic status on phenetic grounds, and there are no phylogenetic reasons for according it more than subgeneric status.

The species *carbonarius* was formerly treated as a member of the subgenus *Gynandrotarsus* because of its trifid foretibial apical spur. However, as explained in the discussion section on the subgenus *Anisodactylus*, this species belongs in the nominate subgenus.

Key to the Species of the Subgenus *Gynandrotarsus*

Notes concerning the key.

Couplet 1 divides the species into 2 groups based primarily on presence or absence of a clypeo-ocular prolongation from the frontal fovea. All sections of each half of the couplet should be read before deciding in which group a given specimen belongs. The clypeo-ocular prolongation described in the first half of the couplet is varied in shape and direction as is the frontal fovea. In most specimens the fronto-clypeal suture as shown in Fig. 7 extends into the frontal fovea and then continues towards the eye as a linear depression or groove constituting the clypeo-ocular prolongation.

The presence or absence of a humeral tooth is used in couplets 8, 12, and 13; the humerus should be examined from directly above to determine if a tooth is present.

In couplet 8 males of *anthracinus* and *merula* are separated from males of *ovularis* and *darlingtoni* primarily by possessing a humeral tooth. I saw 3 males of *anthracinus* (all from Arizona), out of a total of approximately 200 males examined, which lacked a humeral tooth. Thus, approximately 1.5 percent of the male *anthracinus* keying to couplet 8 may be impossible to separate from *ovularis* and *darlingtoni* on the basis of only the humeral tooth character. Therefore, additional information has been provided on the median lobe of the species keying to couplet 8 to insure 100 percent correct determination of male *anthracinus*. The reader should also note that if the specimen is from southwestern Texas or Arizona, it probably is an *anthracinus* (whether a humeral tooth is present or not) since the other 3 species mentioned above are not recorded from these areas. I have not seen any Mexican specimens of *anthracinus* which lack a humeral tooth.

Some difficulty may be encountered in determining whether a humeral tooth is present on females of *merula* and *rusticus* which key to couplet 12. This is because occasional specimens of *rusticus* have a small primarily upward directed humeral denticle. When the humerus is examined in dorsal view, the denticle is not very evident in most specimens. I have seen 5 females with a vestigial laterally directed tooth and could not classify them to species since presence or absence of a humeral tooth is the sole known character of use in separating females of *rusticus* and *merula*.

The presence of a humeral tooth is used in couplet 13 to separate female *anthracinus* from female *ovularis* and *darlingtoni*. I have not yet encountered any females of *anthracinus* lacking a humeral tooth, but if the reader encounters a specimen which gives problems in this couplet, geographical distributions should be consulted. The range of *ovularis* is north

of those of *anthracinus* and *darlingtoni*, and of these 3 species only *anthracinus* is so far recorded from southwestern Texas and Arizona. The species *anthracinus* and *darlingtoni* are sympatric in Mexico. Many specimens of *darlingtoni* have a somewhat more slender body form than those of *anthracinus*. However, this slight difference in body form is not easy to note without large series of each species and is not as consistent or reliable for separating *anthracinus* and *darlingtoni* as presence or absence of a humeral tooth. No other characters are of practical use for separating females of these 2 species.

Key to the Species of the Subgenus Gynandrotarsus

- 1 Frontal fovea of head with clypeo-ocular prolongation toward eye (Fig. 46); OR clypeus lacking raised transverse ridge behind apex 2
- Frontal fovea of head lacking clypeo-ocular prolongation; AND clypeus with raised transverse ridge behind apex 5
- 2 (1) Dorsum dull black, not shiny, with prominent microsculpture; clypeus with raised transverse ridge behind apex; median lobe extremely narrow in lateral view, without apical disc (Figs. 111, 112); first segment of foretarsus of ♀ strongly expanded laterally (Fig. 43) *opaculus* (LeConte), p. 358
- Dorsum shiny, microsculpture less developed; clypeus with or without raised transverse ridge behind apex; median lobe not as narrow (Figs. 118, 120, 124); first segment of foretarsus of ♀ various 3
- 3 (2) Clypeus with raised transverse ridge behind apex; posterior pronotal angle not broadly rounded (Fig. 32); first segment of foretarsus of ♀ moderately expanded laterally (Fig. 42) *texanus* (Schaeffer), p. 361
- Clypeus without raised transverse ridge behind apex; pronotal posterior angle various (Figs. 28, 31) 4
- 4 (3) Dorsum with prominent greenish tinge, especially towards sides; abdominal sternum VI of ♂ with 2 pairs of ambulatory setae; median lobe without apical disc (Figs. 123, 124); first segment of foretarsus of ♀ very strongly expanded laterally, overlapping ventral base of segment II (Fig. 44) *harpalooides* (LaFerté), p. 360
- Dorsum without prominent greenish tinge; abdominal sternum VI of ♂ with 1 pair of ambulatory setae; median lobe with prominent apical disc (Figs. 117, 118); first segment of foretarsus of ♀ only slightly expanded laterally (Fig. 41) *dulcicollis* (LaFerté), p. 362
- 5 (1) Pronotal lateral bead fine basally and medially, obsolescent near anterior angle (Fig. 34); microsculpture of frons and pronotum consisting of very dense small isodiametric punctures; median lobe with apical disc (Figs. 113, 114) *haplomus* Chaudoir, p. 363
- Pronotal lateral bead more prominent basally and medially, not obsolescent (though fine in some specimens) near anterior angle; microsculpture of frons consisting of isodiametric mesh, not of punctures; microsculpture of pronotum various, of isodiametric mesh in most specimens; median lobe with or without apical disc 6
- 6 (5) Males, segments II to IV of fore- and midtarsus laterally expanded and spongy pubescent beneath 7
- Females, segments II to IV of fore- and midtarsus neither laterally expanded or spongy pubescent beneath 11
- 7 (6) Median lobe lacking apical disc (Figs. 115, 116) (in part) *rusticus* (Say), p. 364
- Median lobe with apical disc (Figs. 109, 110, 121, 122, 125, 126) 8

8 (7) Humerus in dorsal view with laterally projected tooth (Fig. 37); median lobe with left side of apical disc not elevated in dorsal view and membranous area of dorsum short (Figs. 121, 122) 9

— Humerus in dorsal view lacking tooth (Fig. 36); median lobe with left side of apical disc elevated in dorsal view and membranous area of dorsum short (Figs. 125, 126) OR median lobe with left side of apical disc not elevated and membranous area of dorsum relatively long, extended in many specimens to basal bulb (Figs. 109, 110) 10

9 (8) Body strongly convex, especially pronotum; pronotum not prominently widened basally and lateral depression not prominent (Fig. 30); range Davis Mts. of extreme western Texas, Arizona, New Mexico and Mexico (Fig. 160)
..... (in part) *anthracinus* (Dejean), p. 366

— Body not strongly convex; pronotum prominently widened basally and with prominent lateral depression rapidly widened basally (Fig. 29); range southeastern Canada, eastern United States (Fig. 161)
..... (in part) *merula* (Germar), p. 368

10 (8) Apical disc of median lobe shaped as in Fig. 125 and with left side slightly elevated in dorsal view; median lobe with membranous area of dorsum relatively short and shaft not strongly bent near basal bulb (Fig. 126); range southeastern Canada, eastern United States (Fig. 163)
..... (in part) *ovularis* (Casey), p. 372

— Apical disc of median lobe shaped as in Fig. 109 and with left side not elevated in dorsal view; median lobe with membranous area of dorsum relatively long, extended to basal bulb (Fig. 110) in many specimens; range northern and central Mexico (Fig. 157) (in part) *darlingtoni* new species, p. 370

11 (6) Pronotum prominently widened basally (Figs. 27, 29) 12

— Pronotum not prominently widened basally, side more evenly curved from apex to base (Figs. 26, 30, 35) 13

12 (11) Humerus in dorsal view with prominent laterally directed tooth projected in most specimens well beyond outer edge of humerus (Fig. 37)
..... (in part) *merula* (Germar), p. 368

— Humerus in dorsal view without prominent laterally directed tooth (Fig. 36); in some specimens with slight mainly upward directed denticle (see discussion of characters used in this key) (in part) *rusticus* (Say), p. 364

13 (11) Humerus in dorsal view with prominent laterally directed tooth projected in most specimens beyond lateral margin of humerus (Fig. 37)
..... (in part) *anthracinus* (Dejean), p. 366

— Humerus in dorsal view lacking tooth 14

14 (13) Range southeastern Canada, eastern United States (Fig. 163); pronotum of many specimens with prominent lateral depression (Fig. 26)
..... (in part) *ovularis* (Casey), p. 372

— Range northern and central Mexico (Fig. 157); pronotum without prominent lateral depression (Fig. 35) (in part) *darlingtoni* new species, p. 370

27.1 *Anisodactylus (Gynandrotarsus) opaculus* (LeConte)
(Figs. 33, 43, 46, 111, 112, 158)

Gynandrotarsus opaculus LeConte, 1863: 16. [Holotype (MCZ), ♀ labeled: blood red disc without printing; "opaculus 2". TYPE LOCALITY: Texas as originally cited].

Triplectrus paulus Casey, 1924: 130. [Lectotype (USNM), here designated, ♂ labeled: "Tex", "Casey bequest 1925", "TYPE USNM 47942", "paulus Csy.". Additional label added stating: "LECTOTYPE *Triplectrus paulus* Casey By G. R. Noonan". TYPE LOCALITY: Austin, Texas as originally cited. NEW SYNONYMY].

Description. — Body length 8.6 to 12.2 mm.

Color. Dorsum black, dull due to prominent microsculpture, with faint greenish hue in some specimens; margins of labrum, clypeus and pronotum slightly lighter in some specimens. Venter, legs, and elytral epipleuron rufopiceous to black. Palpi and first 1 or 2 antennal segments rufotestaceous to piceous or castaneous; remaining antennal segments darker in most specimens.

Head. Labral apex straight to moderately emarginate medially. Clypeus with area immediately behind apex slightly elevated into low ridge and sloped proximally into shallow, fine groove; apex straight to moderately emarginate medially. Frons with fovea punctiform, bearing clypeo-ocular prolongation; microsculpture of prominent isodiametric mesh. Mental tooth absent to prominent.

Thorax. Pronotum as in Fig. 33; lateral depression obsolescent to moderate; lateral bead moderately prominent; basal fovea shallow, linear to elliptical; microsculpture of prominent isodiametric mesh.

Legs. Dorsum of tarsi glabrous to sparsely pubescent. Foretarsus of ♀ with segment I strongly expanded laterally (Fig. 43) but not as greatly as in *harpaloides*.

Elytron. Humerus (posterior aspect) of most specimens with rudimentary tooth; intervals flat to slightly convex; stria moderately prominent in most specimens; subapical sinuation obsolescent or absent; microsculpture of prominent slightly granulate isodiametric mesh.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae.

Male genitalia. Median lobe (Figs. 111, 112) very narrow in lateral aspect; without apical disc; membranous area of dorsum short in most specimens. Everted internal sac with distal portion bearing varied series of scale-like spines similar to those in *dulcicollis*.

Variation. — Intrapopulational variation occurs in: color; body size and to a slight degree body proportions; emargination of labral and clypeal apices; presence or absence of mental tooth; prominence of pronotal lateral depression; humeral tooth; convexity of elytral intervals; prominence of elytral stria and subapical sinuation; and number and arrangement of scale-like spines on internal sac.

Discussion. — The LeConte collection at MCZ contains a series of 8 *opaculus*. The first specimen is a male labeled: blood red disc without printing, "7", "Type 5948", "C. *opaculus* Salle Lec.". This specimen cannot be the holotype since LeConte said his single specimen was a female given to him by a Mr. Ulke and stated "the terminal spur of the anterior tibiae is broken. . .". The male specimen labeled as a type evidently came from Salle and has both terminal spurs intact. The second specimen is a female labeled: blood red disc without printing, "opaculus 2". This specimen has both terminal spurs broken (only specimen in the series with the spurs so damaged), fits LeConte's description, and is the true holotype.

The form *paulus* was distinguished from *opaculus* by Casey (1924) on the basis of smaller body size, shorter prothorax, deeper and coarser elytral stria, more convex elytral intervals, and smaller head. These characters vary within *opaculus*, and the lectotype of *paulus* bears no characters warranting separate status from *opaculus*.

Flight. — Members of this species have been taken frequently at lights throughout its range and apparently are ready fliers.

Bionomics. — Members of this species have been collected from January to August and in November but appear to be most common in June, July and August.

Ball's data indicate *opaculus* has been taken: in dry leaf litter on damp soil in woods of

hackberry trees with varied rather open undergrowth on the Blackstone Ranch, 16 mi. S. of Sheffield, Texas; and Ball has collected specimens as they crawled at dusk over bare dry ground in an area of scrub desert with mesquite on the Blackstone Ranch, 13 mi. S. of Sheffield, Texas. Label data on specimens indicate that: 1 female was found in the soil of a peach orchard in Caddo County, Louisiana; 2 females were taken along a pond margin 5 mi. N. of Dilley, Texas; 2 males, 2 females were collected in pit fall traps in a region of tall grass in Davis County Arkansas; 1 male was taken under stones at Gainesville, Texas; and 1 female from under dried cow chips at Victoria, Texas.

Forbes (1883) reported that the gut contents of 2 specimens of *opaculus* consisted of seeds and other vegetable matter.

Distribution and material examined (699 specimens). The species *opaculus* is found in the south central United States, and 1 specimen has been taken in Mexico, 5 mi. W. Iturbide, Nuevo Leon (Fig. 158). I have also seen 2 specimens labeled as being from Long Island, New York, but believe they are mislabeled since this is far north of the established range.

27.2 *Anisodactylus (Gynandrotarsus) harpaloides* (LaFerté)
(Figs. 31, 44, 123, 124, 159)

Gynandrotarsus harpaloides LaFerté, 1841a: 203. [Lectotype (MNHP), here designated, ♀ labeled: "harpaloides m. Po. in Texas.", "Ex Musaeo Chaudoir". Additional label added stating: "LECTOTYPE Gynandrotarsus harpaloides LaFerte By G. R. Noonan". TYPE LOCALITY: Texas as originally cited].

Triplectrus beryllus Casey, 1924: 131. [Lectotype (USNM), here designated, ♂ labeled: "McPher Ks", "Casey bequest 1925", "TYPE USNM 47973", "beryllus Cs."]. Additional label added stating: "LECTOTYPE Triplectrus beryllus Casey By G. R. Noonan". NEW SYNONYMY].

Description. — Body length 8.2 to 10.9 mm.

Color. Dorsum piceous to black, margins of labrum, clypeus, and pronotum lighter in some specimens; center of frons with rufescent spot in some specimens; head and pronotum of some specimens with greenish tinge, such tinge more prominent along pronotal sides and in area of pronotal basal fovea; elytron of most specimens with prominent greenish tinge. Venter and coxae rufopiceous to black. Trochanters, femora, tibiae, palpi and first 1 or 2 antennal segments testaceous to rufopiceous or castaneous; tarsi and remainder of antenna darker in most specimens.

Head. Labral and clypeal apices straight to slightly emarginate medially. Frons with fovea punctiform, bearing clypeo-ocular prolongation; microsculpture of isodiametric mesh, obsolescent medially in most specimens. Mentum without tooth.

Thorax. Pronotum (Fig. 31) with anterior angle somewhat less prominent than in *dulcicollis*; posterior angle moderately rounded; lateral depression obsolescent in most specimens; lateral bead prominent; basal fovea shallow, linear to slightly elliptical, in most specimens with scattered punctures; microsculpture of isodiametric mesh, obsolescent medially in most specimens.

Legs. Foretarsus of ♀ with segment I very strongly expanded laterally, plate-like, and overlapping ventral base of segment II (Fig. 44).

Elytron. Humerus without tooth; intervals flat to slightly convex; subapical sinuation obsolescent; microsculpture of isodiametric mesh.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae.

Male genitalia. Median lobe (Figs. 123, 124) relatively slender; without apical disc; membranous area of dorsum short to long, in some specimens extended nearly to basal bulb;

ventral and lateral sides with longitudinal striae in most specimens. Everted sac bearing proximal very discrete field of scale-like spines and apical less sharply defined field of scale-like spines.

Variation. — Intrapopulational variation exists in: body size; color; and emargination of labral and clypeal apices.

Discussion. — I have examined the male lectotype, 2 male paralectotypes and the female paralectotype of *beryllus*. All four specimens have a conspicuous greenish tinge to the dorsum and lack a raised ridge behind the clypeal apex. The males have the form of median lobe found only in *harpaloides* while the female has the first segment of the foretarsus very strongly expanded laterally. There is no reason to regard *beryllus* as a separate species.

Bionomics. — Members of this species have been collected in January and from March to September. As discussed under the species *dulcicollis*, I collected *harpaloides* in association with *dulcicollis* and *ovularis* in a pasture 2.7 mi. W. of Millington, Tennessee on September 16, 1969. All of the *harpaloides* were slightly teneral. Label data on the material examined indicate that *harpaloides* has been taken as follows: 1 female in sedge grass, Arkansas County, Arkansas; 1 male associated with cotton, Jefferson County, Arkansas; and 1 male and 1 female under a stone, Atchison County, Kansas.

Distribution and material examined (62 specimens). This species is known from Arkansas, Florida, Kansas, Louisiana, Oklahoma, Missouri, Tennessee, and Texas (Fig. 159).

27.3 *Anisodactylus (Gynandrotarsus) texanus* Schaeffer (Figs. 32, 42, 119, 120, 164)

Anisodactylus (Triplectrus) texanus Schaeffer, 1910: 404. [Lectotype (USNM), here designated, ♂ labeled: "N. Braunfels, Tex.". Additional label added stating: "LECTOTYPE Anisodactylus texanus Schaeffer By G. R. Noonan". TYPE LOCALITY: New Braunfels, Texas as originally cited].

Description. — Body length 9.5 to 12.2 mm.

Color. Dorsum shiny dark piceous to black; margins of labrum, clypeus, and pronotum lighter in some specimens. Venter and legs piceous to black. Palpi rufous to black or infuscated. Antenna with segment I testaceous to rufopiceous; remaining segments somewhat darker.

Head. Labral apex straight to slightly emarginate medially. Clypeus with apex straight to slightly emarginate medially; raised transverse ridge present behind apex. Frons with fovea punctiform, bearing clypeo-ocular prolongation; microsculpture of isodiametric mesh, obsolete medially. Mentum without tooth.

Thorax. Pronotum (Fig. 32) with posterior angle slightly obtuse, not broadly rounded as in *dulcicollis*; lateral depression obsolescent; lateral bead prominent, especially near posterior angle; basal fovea shallow, linear to slightly elliptical, with scattered punctures in most specimens; microsculpture obsolescent medially, elsewhere of isodiametric mesh.

Legs. Dorsum of tarsi glabrous in most specimens. Foretarsus of ♀ with segment I moderately expanded laterally (Fig. 42).

Elytron. Humerus (in posterior aspect) of most specimens with rudimentary tooth; intervals flat to moderately convex; subapical sinuation obsolescent; microsculpture isodiametric, nearly obsolescent in ♂, normal in ♀.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae.

Male genitalia. Median lobe (Figs. 119, 120) with prominent apical disc; dorsum of apex between distal end of membranous area and apical disc concave and laterally bounded by raised ridge formed from sides of median lobe. Everted internal sac bearing varied armature,

consisting in most specimens of proximal field of moderate sized scale-like spines and more distally situated fields of small scale-like spines.

Discussion. — The collection at USNM contains several specimens with written labels stating "N. Braunfels, Tex." The handwriting on the labels may well be that of Schaeffer (Kenneth Cooper, personal communication). Lindroth (1968) reported he could not locate types of *texanus* at the USNM. I feel these specimens are part of the original type series and have (above) designated one as the lectotype.

Flight. — One female was taken by light at Boquillas in Big Bend National Park, Texas.

Bionomics. — Members of this species have been collected from February to August. Ball's data indicate specimens have been taken: under stones on damp ground with sparse vegetation near small water impoundment in desert region on the Cochran Ranch, Sanderson, Texas; under cover of bent, coarse grass, tree branches, and stones along roadside ditch and depression filled with water by recent rains in normally arid region 16 mi. N. of Dryden, Texas; in dry leaves on damp clay soil in a stand of evergreen oaks near Independence Creek in the vicinity of the Pecos River, Texas; in dry leaf litter on damp soil in woods of hackberry trees with varied rather open undergrowth 16 mi. S. Sheffield; as beetles crawled over surface of bare dry ground at dusk in scrub desert with mesquite 13 mi. S. Sheffield, Texas; and under stones in gravel pit on slight slope in desert region with acacia shrubs and few grasses at Villa Lopez, Mexico.

Distribution and material examined (109 specimens). This species is found in southern Arizona, Louisiana, Texas, and northern Mexico (Fig. 164).

27.4 *Anisodactylus (Gynandrotarsus) dulcicollis* (LaFerté)

(Figs. 28, 41, 45, 117, 118, 165)

Harpalus dulcicollis LaFerté, 1841b: 44. [Lectotype (MNHP), designated by Lindroth (1968 and 1969a), ♂ labeled: "Ex Musaeo Chadoir", "TYPE". TYPE LOCALITY: Texas as originally cited].

Anisodactylus (Triplectrus) ellipticus LeConte, 1848: 384. [Type (MCZ), ♂ labeled: orange disc without printing, "Type 5967", "A. ellipticus Lec", "dulcicollis 6". TYPE LOCALITY: New Orleans, Louisiana as originally cited].

Anisodactylus (Gynandrotarsus) elongatus Chadoir, 1868: 163. [Holotype (MNHP), ♂ labeled: "Ex Musaeo Chadoir", "Texas Salle.", "TYPE", "dulcicollis Laf. det Lindroth 67". TYPE LOCALITY: Texas as originally cited].

Triplectrus modicus Casey, 1914: 178. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♀. TYPE LOCALITY: Houston, Texas as originally cited].

Description. — Body length 8.5 to 11.8 mm.

Color. Dorsum somewhat shiny, especially on pronotum, black or very dark piceous; in some specimens margins of labrum, clypeus, and pronotum lighter; pronotal sides translucent in some specimens; elytron with faint aeneous tinge in some specimens. Venter, legs, and elytral epipleuron rufopiceous to black. Palpi and first 2 antennal segments testaceous to rufotestaceous or castaneous; remaining antennal segments same or slightly darker.

Head. Labral and clypeal apices straight to slightly emarginate medially. Mentum without tooth or small tooth present. Frons with fovea punctiform, in most specimens bearing clypeo-ocular prolongation; microsculpture of isodiametric mesh, obsolete medially in many specimens.

Thorax. Pronotum (Fig. 28) with prominent anterior angle; posterior angle broadly rounded; lateral depression obsolescent; lateral bead moderately prominent; basal fovea shallow, linear to elliptical, with scattered punctures in most specimens; microsculpture obsolescent

medially, elsewhere of isodiametric mesh.

Legs. Dorsum of tarsi glabrous to sparsely pubescent. Foretarsus of ♀ with segment I slightly expanded laterally (Fig. 41).

Elytron. Humerus (posterior aspect) of some specimens with faint rudimentary tooth; intervals flat to slightly convex; subapical sinuation obsolescent; microsculpture of isodiametric mesh, slightly granulate in ♀.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae.

Male genitalia. Median lobe (Figs. 117, 118) in dorsal view with sides somewhat parallel just before apex; with prominent apical disc; ventral surface with prominent longitudinal striae in many specimens. Internal sac relatively long and in repose irregularly coiled within median lobe; everted sac showing several large scale-like spines near distal end and bearing various very small spines and scales.

Variation. — Intrapopulational variation occurs in: body size; color; emargination of labral and clypeal apices; mental tooth; pronotal basal fovea; humeral tooth; convexity of elytral intervals; striae of median lobe; and number and arrangement of large scale-like spines and small spines and scales on internal sac.

Discussion. — The forms *ellipticus*, *elongatus* and *modicus* were correctly treated as conspecific with *dulcicollis* by Lindroth (1968).

Flight. — Specimens of *dulcicollis* have been collected at lights throughout its range and are evidently ready fliers.

Bionomics. — Members of this species have been taken from throughout the year but appear to be most common during April to August.

On October 16, 1969, I collected 14 males and 11 females of *dulcicollis* in a pasture 2.7 mi. W. Millington, Tennessee. The species was associated with *harpaloides* and *ovularis* and together with them was restricted to the tops and sides of small hills where the ground was well drained, exposed to sun during the entire day, and covered with only a sparse growth of short grass. All of the specimens of these 3 species were found during the day resting on the surface of the ground (or in short tunnels just below the surface) beneath dried cow chips. I also collected in well drained areas receiving shade from trees but found no *Gynandrotarsus* in such areas. Other areas of the pasture which received sun all day but were less well drained and had a denser grass cover also contained no *Gynandrotarsus*.

Label data indicate specimens have been taken: from pit fall traps in regions of tall grass at several localities in Louisiana; from cultivated lands such as strawberry fields, cottonfields, peach orchards, rice levies, gardens and sweet potato fields; under bark of rotting logs; under *Opuntia*; in pastures; under stones; and associated with trash.

Distribution and material examined (420 specimens). This species is found in the southern and central part of the eastern United States (Fig. 165). I have also seen 1 specimen labeled as from the Huachuca Mts. of Arizona, 1 labeled as from Los Angeles County, California, and 1 labeled as from Colorado.

27.5 *Anisodactylus (Gynandrotarsus) haplomus* Chaudoir (Figs. 34, 113, 114, 166)

Anisodactylus (Gynandrotarsus) haplomus Chaudoir, 1868: 163. [Holotype (MNHP), ♀ labeled: "bor", "Ex Musaeo Chaudoir", "Type". TYPE LOCALITY: Not originally cited, Galveston, Texas designated by Lindroth (1968)].

Triplectrus peropacus Casey, 1914: 175. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♂. TYPE LOCALITY: Galveston, Texas to District of Columbia originally cited, restricted to Galveston, Texas by Lindroth (1968)].

Triplectrus breviceps Casey, 1924: 129. [Holotype (USNM), ♀. TYPE LOCALITY: Mobile, Alabama as originally cited].

Triplectrus longicollis Casey, 1924: 129. [Holotype (USNM), ♂ labeled: "D.C.", "Casey bequest 1925", "TYPE USNM 47973", "longicollis Csy.". TYPE LOCALITY: District of Columbia as originally cited. NEW SYNONYMY].

Description. — Body length 9.9 to 15.0 mm.

Color. Dorsum black, margins of labrum lighter in some specimens. Venter and legs rufopiceous to black. Palpi rufopiceous to black or infuscated. Antenna with first 1 or 2 segments testaceous to rufopiceous; remaining segments darker in most specimens.

Head. Labral apex straight to moderately emarginate medially. Clypeus with apex straight to slightly emarginate medially; with transverse raised ridge immediately behind apex. Frons with fovea punctiform; microsculpture of small dense isodiametric punctures. Mentum of most specimens without tooth.

Thorax. Pronotum (Fig. 34) widened basally; anterior margin somewhat less emarginate and anterior angle more rounded than in *rusticus*; lateral depression relatively wide, especially basally, not sharply delimited, evident to anterior angle; lateral bead fine, becoming obsolescent just behind anterior angle; basal fovea shallow, irregular or linear, in most specimens with few scattered punctures; microsculpture as on frons.

Elytron. Humerus without tooth; intervals slightly to strongly convex; subapical sinuation prominent and deep; microsculpture of isodiametric punctures, under certain lighting conditions appearing as granulate mesh.

Abdomen. Sternum VI of ♂ with 1 or 2 pairs of ambulatory setae.

Male genitalia. Median lobe (Figs. 113, 114) with apical disc; dorsum between distal end of membranous area and apical disc slightly convex; apex bent ventrad; membranous area of dorsum short, not reaching basal bulb.

Variation. — Intrapopulational variation exists in: body size; color; emargination of labral and clypeal apices; presence or absence of mental tooth; convexity of elytral intervals.

Discussion. — The forms *peropacus* and *breviceps* were correctly treated by Lindroth (1968) as conspecific with *haplomus*; their types have: pronotal lateral bead obsolescent near anterior angle; pronotal microsculpture of isodiametric punctures; humerus without tooth; and elytral subapical sinuation prominent. The form *longicollis* was said by Casey to differ from *peropacus* by being narrower and smaller and having the anterior male tarsi less strongly dilated; but these characters vary somewhat within *haplomus*, and the type of *longicollis* possesses the characters of *haplomus*.

Flight. — Members of this species have been taken at light in May and June at a number of localities and are apparently ready fliers.

Bionomics. — Members of this species have been collected in March to August, November, and December but appear to be most common in May and June.

Distribution and material examined (193 specimens). This species is known from scattered localities in eastern United States (Fig. 166).

27.6 *Anisodactylus (Gynandrotarsus) rusticus* (Say)

(Figs. 27, 40, 115, 116, 162)

Harpalus rusticus Say, 1823: 32. [Neotype (MCZ), designated by Lindroth (1969b), ♂ labeled: "Rumney, N. H. VI-30 1924 Baker R.", "♂", "P. J. Darlington Collection", "Neotype Harpalus rusticus Say design. Lth.", "Anisodactylus rusticus Say det. Lindroth 68.". TYPE LOCALITY: Not originally cited, restricted to Rumney, New Hampshire by Lindroth (1968)].

Anisodactylus tristis Dejean, 1829: 158. [Lectotype (MNHP), here designated, ♂ labeled: “♂”, “tristis. m. in Amer. bor.”, “Beauvois”, “Anisod. rusticus Say. box 207.”. Additional label added stating: “LECTOTYPE Anisodactylus tristis Dejean By G. R. Noonan”. TYPE LOCALITY: “Amer. sept.” originally cited].

Triplectrus oblongus Casey, 1924: 128. [Holotype (USNM), ♀. TYPE LOCALITY: Nisbet, Pennsylvania as originally cited].

Description. — Body length 7.2 to 12.6 mm.

Color. Dorsum rufopiceous to black; margins of labrum, clypeus, and pronotal base lighter in some specimens; in most specimens sides of pronotum rufescent or translucent, especially posteriorly. Venter rufopiceous to black. Legs rufopiceous to black, in most specimens femora darker than other segments. Palpi testaceous to black or infuscated, apices lighter in most specimens. Antenna with first 2 segments testaceous or rufous in most specimens, infuscated in a few specimens; remaining segments darker in most specimens.

Head. Labral apex slightly to moderately emarginate medially. Clypeus with apex moderately to strongly emarginate medially, base of labrum exposed in some specimens; transverse ridge present behind apex. Frons with fovea punctiform; microsculpture of prominent isodiametric mesh. Mentum of most specimens without tooth.

Thorax. Pronotum (Fig. 27) prominently widened basally; lateral depression prominent, strongly widened basally; lateral bead moderate, in most specimens narrowed just before posterior angle; basal fovea various, linear or elliptical in many specimens; microsculpture medially of isodiametric mesh, elsewhere appearing as isodiametric punctures or slightly granulate mesh depending on lighting.

Elytron. Humerus (in dorsal view) without tooth except for few specimens possessing vestigial tooth (see discussion under variation); intervals flat to strongly convex; subapical sinuation obsolescent; microsculpture of isodiametric punctures with tendency to be arranged in irregular chains.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae.

Male genitalia. Median lobe (Figs. 115, 116) without apical disc; tip bent ventrad in many specimens.

Variation. — Intrapopulational variation exists in: body size; color; microsculpture; emargination of labral and clypeal apices; pronotal basal fovea; and convexity of elytral intervals. I have seen 4 males with vestigial humeral teeth, but they clearly are *rusticus*; their median lobes lack apical discs. The 4 specimens are from: Mt. Toby Massachusetts; E. Hartford, Connecticut; Rockaway Beach, Long Island, New York; and Clemson, South Carolina. In addition, I have seen 5 females with vestigial humeral teeth; they may be either *merula* or aberrant *rusticus*. These females are from: Berryville, Arkansas; Prospect Park, Long Island, New York; Dallas, Texas; Mt. Mitchel, North Carolina; and Washington County, Arkansas.

Discussion. — The form *tristis* has correctly been regarded as conspecific with *rusticus* since shortly after its description. Further, the form *oblongus* was correctly treated as conspecific with *rusticus* by Lindroth (1968). Possible problems in separating aberrant specimens of *rusticus* from specimens of *merula* are treated in the introduction to the species key.

Flight. — Lindroth (1968) reported *rusticus* as being “Found in great numbers in wind-drift material on the north-shore of L. Erie. . . certainly a good flier.” One female was taken in March as it flew in a pasture south of Creedmoor, Granville County, North Carolina. One female and 1 male were taken in April and August respectively at lights at Nevada, Vernon County, Missouri. Three females were taken at electric lights in April, May, and June at Washington, D.C.

Bionomics. — Members of this species have been taken throughout the entire year but

appear to be most common in May to August. Lindroth (1968) reported *rusticus* is found "On dry, sandy fields with thin but often tall vegetation. During daytime hiding under the plants."

In May I took 9 males and 9 females in an old gravel pit at Forestville, Maryland, 6.2 mi. W. of Washington, D. C. The specimens were found on moist gravel soil beneath debris in areas receiving sun throughout the entire day. The ground had a very scattered and sparse grass cover. In July T. and L. Erwin and I (as described under the species *ovularis*) collected 5 males of *rusticus* along with a female *ovularis* on the edge of a grassy field 4.1 mi. W. of Paris, Clarke County, Virginia.

Label data on material examined indicates *rusticus* has been taken: in sand dunes west of Johnson, Vermont; in a gravel pit at Middlebury, Vermont; on soil under dead grass in a peach orchard in Stoddard County, Missouri; from a 5 year old *Pinus sylvestri* plantation in Wexford County, Michigan; under debris on the shore of Lake Michigan, Michigan; in grassland at Manhattan, Kansas; in broom sedge in White County, Arkansas; in cotton in Pope County, Arkansas; in areas of Karmax and Amiban grass in Washington County, Arkansas; under corn stalks near Ethylsville, Alabama; and washed up at Rockaway Beach, Long Island, New York.

Johnson and Cameron (1969) reported that a specimen of *rusticus* fed on grass seed in the laboratory.

Distribution and material examined (1,150 specimens). This species is centered in eastern United States and southeastern Texas (Fig. 162). It ranges from Prince Edward Island (Lindroth, 1968) in the northeast to Yellowstone National Park, Wyoming (2 males) and Greeley, Weld County, Colorado (1 female) in the northwest, southward to Arizona (Casey, 1924) and south to Cuero, De Witt County, Texas (1 female).

27.7 *Anisodactylus (Gynandrotarsus) anthracinus* (Dejean)
(Figs. 30, 37, 160)

Harpalus anthracinus Dejean, 1829: 369. [Holotype (MNHP), ♀ labeled: "♀", "Harpal", "anthracinus. m in Mexico", "Höpfner", "Ex Musaeo Chaudoir", "Bates vidit 1881".
TYPE LOCALITY: Mexico as originally cited].

Anisodactylus dilatatus Say, 1834: 431. [Neotype (MCZ), here designated, ♂ labeled: "37 mi. west of Durango, DGO. 8400'. 3 18 1963 W.S. Creighton". Additional label added stating: "Neotype Anisodactylus dilatatus design. G. R. Noonan".
TYPE LOCALITY: Mexico cited by Say, here restricted to 37 mi. W. Durango, Durango, Mexico].

Triplectrus convexus Casey, 1914: 176. [Lectotype (USNM), here designated, ♂ labeled: "Ari.", "Casey bequest 1925", "TYPE USNM 47938", "convexus Csy.". Additional label added stating: "LECTOTYPE Triplectrus convexus Casey By G. R. Noonan".
TYPE LOCALITY: Arizona originally cited, here restricted to Madera Canyon, Pima County, Arizona. NEW SYNONYMY].

Description. — Body length 11.3 to 14.9 mm.

Color. Dorsum dark piceous to black except margins of labrum, clypeus, and pronotum may be lighter. Venter and legs rufopiceous to black. Palpi testaceous to piceous. Antenna with first segment testaceous to piceous; remaining segments darker in most specimens.

Head. Labral apex slightly to moderately emarginate medially. Clypeus with apex slightly to moderately emarginate medially, base of labrum exposed in many specimens; with low transverse ridge behind apex. Frons with fovea punctiform, in some specimens bearing medially directed impression; microsculpture of isodiametric mesh, may be obsolescent medially, especially in ♂; surface may be wrinkled. Mentum without or with slight tooth.

Thorax. Pronotum (Fig. 30) very convex (much more so than in *merula*; not prominently widened basally; lateral bead moderate; surface wrinkled in some specimens; basal fovea various, in many specimens linear or elliptical; microsculpture of isodiametric mesh, obsolete medially in many specimens, especially in ♂).

Elytron. Humerus (in dorsal view) with tooth (Fig. 37) (except for 3 ♂♂ as mentioned in section on variation); intervals flat to moderately convex; subapical sinuation obsolescent; microsculpture of isodiametric mesh in ♂, in ♀ appearing either as isodiametric punctures or granulate isodiametric mesh depending on lighting conditions.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae.

Male genitalia. As in *merula*.

Variation. — Intrapopulational variation occurs in: body size; color; microsculpture; emargination of labral and clypeal apices; frontal fovea; pronotal basal fovea; degree of convexity of elytral intervals. One female from 6 mi. E. of Queretaro, Queretaro, Mexico is unique in bearing 2 long setae at the right distal outer angle of the clypeus. The humeral tooth is vestigial and difficult to discern in: a male from 18 mi. S.W. of Bowie, near Apache Pass, Cochise County, Arizona; a male from the eastern slope of the Galiuro Mountains, Graham County, Arizona; and a male from Madera Canyon, Santa Rita Mountains, Arizona. However, all other characters in these 3 males are those "normal" for the species *anthracinus*.

Discussion. — I above designate a neotype for *dilatatus*. The entire insect collection of Say was destroyed except for a few specimens sent to Dejean in France (Lindroth and Freitag, 1969b). The Oberthür collection at the MNHP contains 4 males and 2 females by the name label "dilatatus Say Mexique". However, none of these specimens bear the green labels characteristic of specimens in the Dejean collection or any other indication that they came from the Dejean collection. All but one specimen, a female, belong to the species *anthracinus*. The female belongs to *darlingtoni*, a new species named in this paper. The original description of *dilatatus* provides no worthwhile clues as to which species or even which subgenus of *Anisodactylus* the original *dilatatus* referred to. However, past authors have treated *dilatatus* as conspecific with *anthracinus*, and in the interest of taxonomic stability I select as neotype a specimen which is a member of this species. The neotype is deposited at MCZ.

Casey (1914) separated *convexus* from *anthracinus* primarily by the arrangement of setigerous punctures along the third elytral interval, but this character varies within *anthracinus* and other species of *Gynandrotarsus*. The lectotype and paralectotypes of *convexus* are all clearly members of the species *anthracinus*.

Males of *anthracinus* and *merula*, clearly allopatric forms (Fig. 160, 161), have the same genitalia. To decide relationships I noted their external differences, and compared these external differences with those found in other pairs of closely related species of *Gynandrotarsus*. Specimens of *anthracinus* differ from *merula* by: more convex body; pronotum not prominently widened basally, much more convex than in *merula*, and with narrow or obsolescent lateral depression. Many specimens of the species pairs *merula* and *haplomus* and *rusticus* and *merula* differ no more from one another externally than do *anthracinus* from *merula*. As to the identical genitalia of *merula* and *anthracinus*, there is no *a priori* reason why genitalia must always be different in separate species. The external features separating *anthracinus* and *merula* are constant and are sufficient to warrant retaining *anthracinus* as a valid species.

Flight. — One female was taken at light in August at Peña Blanca, Arizona, and 1 male and 2 females were taken at light in June at the Southwest Research Station, 5 mi. W. Portal, Arizona.

Bionomics. — Members of this species have been taken in January and from March to

November but appear to be most common in June, July, and August. In September of 1964 and 1969, I collected 23 *anthracinus* on or adjacent to Procter's Ranch at the entrance to Madera Canyon, Pima County, Arizona. The area was primarily desert-like with ocotillo, barrel cactus, mesquite, yuccas, and various grasses. During the day specimens were found resting under dried cow chips and rocks. After approximately 17:40 (Pacific Standard Time) they were found mainly crawling over the surface of the ground. All the sites containing *anthracinus* received sun during most of the day. In September, I also took 3 specimens in the collecting area at the Southwest Research Station described under the species *Notioobia brevicollis*.

Ball's data indicate specimens have been taken: under cover on sandy clay soil with grasses in a pinon pine, juniper, and evergreen oak forest in the Davis Mountains, Texas; under cover of stones, leaves, bark, and fallen logs in area with walnut, willow, and poplar trees in Limpia Canyon, Davis Mountains, Texas; under cover on damp, bare clay soil on eastern slope of the Galiuro Mountains, Graham County, Arizona; under dried cow chips on sandy clay soil in grassy meadow with many flowers and some shrubs 18 mi. S.W. Bowie near Apache Pass, Cochise County, Arizona; under rocks on sandy soil in desert scrub area 6 mi. E. Queretaro, Mexico; under stones on reddish clay soil in vicinity of small pond with vegetation of grasses and herbs in semi-desert country 33 km. N. of Acambay, Mexico; under cover on east facing slope with cut-over tropical deciduous forest and grassy meadows below the trees 9.5 mi. W. of Morelia, Mexico; and under *Acacia* shrubs on dam face, in litter, and under cover in unshaded places in area of acacia-grassland mainly in vicinity of small reservoir on west side of road 13 mi. S.E. of Lagos de Moreno, Mexico.

Distribution and material examined (427 specimens). This species is found: in the Davis Mountains of extreme southwestern New Mexico; highland or mountainous areas of Arizona (few specimens seen labeled as from Tucson and Phoenix but probably collected in nearby mountains or else taken at light); Tulare County, California (based on single specimen in Van Dyke Collection at California Academy of Sciences); and in the central and northern highlands of Mexico (Fig. 160). The Mexican part of its range is sympatric with that of *darlingtoni*, and the two species occur together at a number of localities in Mexico.

27.8 *Anisodactylus (Gynandrotarsus) merula* (Germar)
(Figs. 29, 121, 122, 161)

Harpalus merula Germar, 1824: 24. [Lectotype (MNHP), designated by Lindroth (1968 and 1969a), ♀ labeled: "Merula Germar in Amer. bor. D.", "to", "Germar", "Ex Musaeo Chaudoir", "Lectotype merula Germ. design. Lindroth". TYPE LOCALITY: Kentucky as originally cited].

Anisodactylus (Triplectrus) crassus LeConte, 1848: 382. [Lectotype (MCZ), designated by Lindroth (1968 and 1969a), ♀ labeled: pink disc without any printing, "269", "Type 5951", "crassus Lec.", "rusticus 16". TYPE LOCALITY: New York (whether city or state not certain) as originally cited].

Anisodactylus (Triplectrus) gravidus LeConte, 1848: 383. [Lectotype (MCZ), designated by Lindroth (1968 and 1969a), ♀ labeled: pink disc without any printing, "Type 5949", "gravidus Lec.", "rusticus". TYPE LOCALITY: New York (whether city or state not certain) as originally cited].

Anisodactylus (Triplectrus) pinguis LeConte, 1848: 382. [Lectotype (MCZ), designated by Lindroth (1968 and 1969a), ♀ labeled: green disc without any printing, "267", "Type 5950", "A. pinguis Lec.", "rusticus 14". TYPE LOCALITY: "ad Rocky Mountains" as originally cited].

Triplectrus aethiops Casey, 1914: 175. [Lectotype (USNM), here designated, ♀ labeled: "Tex", "Casey bequest 1925", "TYPE USNM 47932", "aethiops Csy". Additional label added stating: "LECTOTYPE *Triplectrus aethiops* Casey By G. R. Noonan". TYPE LOCALITY: Austin and Waco, Texas originally cited, restricted to Austin by Casey in 1924. NEW SYNONYMY].

Triplectrus kempi Casey, 1924: 130. [Holotype (USNM), ♀. TYPE LOCALITY: Lake George, New York as originally cited].

Triplectrus marginatus Casey, 1924: 126. [Holotype (USNM), ♂ labeled: "Mich", Casey bequest 1925", "TYPE USNM 47934", "marginatus Csy". TYPE LOCALITY: Grayling, near Bay City, Michigan as originally cited].

Triplectrus sulcipennis Casey, 1924: 128. [Lectotype (USNM), here designated, ♀ labeled: "Tex Waco", "TYPE USNM 47931", "sulcipennis Csy". Additional label added stating: "LECTOTYPE *Triplectrus sulcipennis* Casey By G. R. Noonan". TYPE LOCALITY: Waco, Texas as originally cited. NEW SYNONYMY].

Triplectrus wolcotti Casey, 1924: 127. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♀. TYPE LOCALITY: Northern Illinois near Chicago as originally cited].

Description. — Body length 9.9 to 14.1 mm. Body less convex than in *anthracinus*. Color. Dorsum rufopiceous to black; margins of labrum, clypeus, and pronotum lighter in some specimens. Venter and legs rufopiceous to black. Palpi testaceous to piceous. Antenna with first 2 segments testaceous to rufopiceous; remaining segments darker in most specimens.

Head. Labral apex slightly to moderately emarginate medially. Clypeus with apex moderately to strongly emarginate medially, base of labrum exposed in some specimens; transverse ridge present behind apex. Frons with fovea punctiform; microsculpture of isodiametric mesh, may be less prominent medially.

Thorax. Pronotum (Fig. 29) not strongly convex; prominently widened basally; lateral depression prominent and rapidly widened basally in most specimens; lateral bead moderate; basal fovea various, in many specimens linear or elliptical; microsculpture in ♂ appearing as isodiametric slightly granulate mesh or as isodiametric punctures depending on lighting, in ♀ appearing as isodiametric granulate mesh or as isodiametric punctures depending on lighting, less prominent medially in many specimens of both sexes but still evident.

Elytron. Humerus (in dorsal view) with tooth (Fig. 37); intervals flat to strongly convex; subapical sinuation obsolescent; microsculpture appearing as granulate isodiametric mesh or isodiametric punctures depending on lighting.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae.

Male genitalia. Median lobe (Figs. 121, 122) rather stout; with prominent apical disc; membranous area of dorsum relatively short and rapidly narrowing proximally, not reaching region of basal bulb.

Variation. — Intrapopulational variation exists in: body size; color; microsculpture; emargination of labral and clypeal apices; pronotal basal fovea; and convexity of elytral intervals.

Discussion. — Lindroth (1968) correctly treated *crassus*, *gravidus*, *pinguis*, *kempi*, *wolcotti*, and *marginatus* as conspecific with *merula*; their types all clearly fall within the boundary of the description given above for *merula*. It is difficult to discern what separating characters Casey (1914) envisioned for *aethiops* other than "form less stout". The type series of *aethiops* was originally composed of 3 specimens. In 1924 Casey split this series and declared the 2 specimens from Austin, Texas to be members of a new species, *sulcipennis*, stated to be broader in form than *aethiops* and to have more convex elytral intervals.

The lectotypes of *aethiops* and *sulcipennis* are neither narrower nor broader than many specimens of *merula* and are clearly members of this species.

Larger examples of *merula* with black body color and microsculpture appearing of isodiametric punctures may resemble *haplomus*. But they are distinguished by the moderately prominent pronotal lateral bead which in *haplomus* is fine basally and obsolescent near the anterior angle.

Flight. — Only 3 specimens are labeled as taken at light: 1 female at an incandescent light in April at Fort Clinch State Park, Florida; 1 female in a light trap at Tyler, Texas; and 1 female at a light at Glen Burnie, Maryland. I have examined 1,134 specimens of *merula* and, therefore, it appears members of this species do not fly readily.

Bionomics. — Members of *merula* have been collected throughout the entire year but seem most common in June, July and August. Lindroth (1968) stated that specimens of *merula* are found "On very dry, sandy ground with scattered vegetation." Label data reveal that specimens have been taken as follows: under rocks and dried cow chips in a number of localities; 1 male, 1 female from *Geomys* burrows 20 mi. S. of San Antonio, Texas; 21 specimens from a *Pinus sylvestris* plantation in Wexford County, Michigan; from soil of peach orchards in Louisiana, Missouri, and North Carolina; in grasslands of Riley County, Kansas; 1 female on cotton in Florida; 1 female on corn at Winnsboro, Louisiana; 1 female under strawberries at Amite, Louisiana; 1 male under stone on dry sandy hill at Billerica, Massachusetts; 1 male under log on dry hillside at Rumney, New Hampshire. One male and 3 females glued on a single card are labeled as having been observed eating eggs of *Pantamorus peregrinus* laid on a small twig.

Distribution and material examined (1,134 specimens). The species *merula* is found along the southeastern boundary of Canada, and in the eastern United States (Fig. 161). The dot in southern California is based on a female labeled as from Anaheim, California (in collection of The Academy of Natural Sciences of Philadelphia). I have seen 3 specimens recorded as from Kentucky, a few from along the margin of Lake Michigan in Illinois and Indiana, and one labeled as from Pennsylvania. Aside from these specimens it seems that *merula* is either absent or very scarce in most of Illinois, Indiana, Ohio, Kentucky, Virginia, West Virginia, Pennsylvania, and eastern New York.

27.9 *Anisodactylus (Gynandrotarsus) darlingtoni* NEW SPECIES (Figs. 35, 36, 109, 110, 157)

Holotype. Male. Mexico, Michoacan Rte. 15, e. Morelia 7000', creek and arid pasture VIII.5.62, H. E. Evans Exp., George E. Ball Collector.

Description. — Body length 10.9 mm.

Color. Dorsum with head black except margins of labrum and clypeus slightly lighter; pronotum black; elytron dark piceous. Venter and legs piceous to black. Palpi rufous to piceous. Antenna with first segment castaneous; remaining ones darker.

Head. Labral apex slightly emarginate medially. Clypeus with apex slightly emarginate medially; raised transverse ridge present behind apex. Frons with fovea punctiform; microsculpture of isodiametric mesh.

Thorax. Pronotum (Fig. 35) with side evenly rounded from apex to base, not widened basally; lateral depression obsolescent; lateral bead moderate; apical bead complete but flattened medially; basal fovea very shallow, linear; microsculpture of isodiametric mesh.

Elytron. Humerus (Fig. 36) (in dorsal view) without tooth; intervals slightly convex; subapical sinuation obsolescent; microsculpture of isodiametric mesh.

Abdomen. Sternum VI bearing 1 pair of ambulatory setae.

Genitalia. Median lobe (Figs. 109, 110) with apical disc; tip of apex bent ventrad; membranous area of dorsum long, extended nearly to basal bulb, relatively wide and occupy-

ing most of dorsal width until near its proximal end.

Allotype. — Female. Same label data as holotype. Body length 12.5 mm. Distal 3 segments of left antenna missing. Microsculpture of dorsum of granulate isodiametric mesh; on elytron each granule with visible depression in center. Sternum VI of abdomen with 2 pairs of ambulatory setae. Genitalia as described for females in subgenus description. Remainder as in holotype.

Paratypes and Variation. — Body length 9.1 to 12.5 mm. The dorsum of some specimens has the pronotal side rufescent, and the second antennal segment of some specimens is light colored as the first. The dorsum is slightly wrinkled in some specimens. The labral and clypeal apices vary from straight to moderately emarginate within populations. The microsculpture of the male and female paratypes is as described respectively for the holotype and allotype. The membranous area of the dorsum of the median lobe is slightly shorter than in the holotype in some males; however, it is always relatively longer and wider than in *merula*. The following paratypes were examined (133 specimens): MEXICO: DISTRITO FEDERAL: San Angel, 5 ♂♂, 2 ♀♀. DURANGO: 25 mi. W. Durango, 1 ♀, VI-29-1964. JALISCO: 13.0 mi. S.E. Lagos de Moreno, Rte. 45, 6,540 feet, reservoir, 1 ♀, IX-7-1967. MEXICO: El Yukon, Rte. 15, W. Toluca, 8,800 feet, 2 ♂♂, 1 ♀, VIII-8-1962; Toluca, 7 ♂♂, 11 ♀♀; 34 km. W. Toluca, Rte. 15, 8,500 feet, 4 ♂♂, creek margin, VIII-9-1962. MICHOACAN: Huajumbaro, Rte. 15, 8,500 feet, 1 ♂, pasture, VIII-5-1962; 4.0 mi. N.W. Jiquilpan, Rte. 110, 5,950 feet, 1 ♀, VIII-2-1967; 13.0 mi. S.E. Lagos de Moreno, Rte. 45, 6,450 feet, 1 ♀, reservoir IX-7-1967; Lago Patzcuaro, 3 ♂♂, 4 ♀♀, VIII-29-1945; E. Morelia, Rte. 15, 7,000 feet, 5 ♂♂, 2 ♀♀, creek and arid pasture, VIII-5-1962; 9.5 mi. W. Morelia, Rte. 15, 6,250 feet, 18 ♂♂, 8 ♀♀, tropical-deciduous forest, VIII-18-1967; 6 km. E. Quiroga, Rte. 15, 7,000 feet, 11 ♂♂, 10 ♀♀, roadside pasture, VIII-6-1962; near Tzintzuntzan, 7,000 feet, 1 ♂, 3 ♀♀, roadside, VIII-6-1962; 50 mi. W. Zitacuaro, 19 ♂♂, 4 ♀♀, IX-19-1938. QUERETARO: 33 km. N. Acambay, Rte. 55, 7,600 feet, 2 ♂♂, 1 ♀, pond and semi-desert, VIII-8-1962. SONORA: Yecora, 7,000 feet, 2 ♂♂, 2 ♀♀, V-20-22-1961. No locality other than country given, 1 ♀.

Deposition of type material. — The holotype and allotype are deposited at MCZ while the paratypes are deposited at CAS, Canadian National Collection at Ottawa, Canada, MCZ, UASM, and USNM.

Derivation of name. — It gives me great pleasure to name this species after P.J. Darlington, Jr., who very kindly offered me encouragement and assistance on numerous occasions.

Flight. — No data available.

Bionomics. — Members of *darlingtoni* have been collected in May, June, August, and September and are most common in August. Label data indicate specimens have been taken at altitudes from 5,950 to 8,500 feet. Ball's data indicate specimens have been collected as follows: the holotype, allotype, and 5 paratypes under stones on north facing slope several feet from small probably intermittent stream in semi-desert grassland east of Morelia; under cover in a cut-over tropical deciduous forest on east facing slope above grassy meadow 9.5 mi. W. of Morelia; under stones on reddish clay soil in vicinity of small pond with vegetation of grasses and herbs in semi-desert country 33 km. N. of Acambay; under stones on damp red clay soil in roadside pasture 6 km. E. of Quiroga; under cover in grassy grazed field with some *Acacia* bushes and black clay soil 4 mi. N.W. Jiquilpan; under *Acacia* bushes on dam face, in litter, and under cover in unshaded places in area of acacia-grassland mainly in vicinity of small reservoir on west side of road 13 mi. S.E. of Lagos de Moreno.

Distribution. — This species is found in the highlands of central and northern Mexico (Fig. 157).

27.10 *Anisodactylus (Gynandrotarsus) ovularis* (Casey)
(Figs. 26, 125, 126, 163)

Triplectrus ovularis Casey, 1914: 177. [Lectotype (USNM), designated by Lindroth (1968 and 1969a), ♂. TYPE LOCALITY: St. Louis, Missouri and Salina, Kansas cited by Casey, restricted to St. Louis, Missouri by Lindroth (1968)].

Triplectrus semirubidus Casey, 1924: 127. [Holotype (USNM), ♀. TYPE LOCALITY: Highland Park, north of Chicago, Illinois as originally cited].

Description. — Body length 9.0 to 13.6 mm.

Color. Dorsum dark piceous to black; margins of labrum and sides of pronotum lighter in some specimens. Venter and legs rufous to black. Palpi and first 2 antennal segments testaceous to rufopiceous or infuscated; remaining segments of antenna darker in most specimens.

Head. Labral apex straight to moderately emarginate medially. Clypeus with apex straight to moderately emarginate medially; area immediately behind apex slightly elevated into low transverse ridge sloped proximally into shallow fine groove. Frons with fovea punctiform; microsculpture of isodiametric mesh. Mentum of most specimens without tooth.

Thorax. Pronotum (Fig. 26) much less widened basally than in *rusticus*, *haplomus*, and most *merula*; side evenly rounded; lateral depression moderate; lateral bead prominent; basal fovea shallow, linear to slightly elliptical in form, with few scattered punctures in most specimens; microsculpture of isodiametric mesh.

Elytron. Humerus without tooth; intervals flat to slightly convex; subapical sinuation obsolescent; microsculpture of dense, mostly triangular punctures, may appear as slightly granulate mesh under certain lighting conditions.

Abdomen. Sternum VI of ♂ with 1 pair of ambulatory setae.

Male genitalia. Median lobe (Figs. 125, 126) relatively elongate and slender; with apical disc; left side of disc in dorsal view slightly more elevated than right side; membranous area of dorsum short; ventral surface in most specimens with prominent longitudinal striae and dorsal surface and sides with obsolescent longitudinal striae.

Discussion. — The holotype of *semirubidus* possesses the pronotal form characteristic for *ovularis*, lacks a humeral tooth, and as determined by Lindroth (1968) is clearly conspecific with *ovularis*.

Flight. — One female was taken at light in June at Glen Burnie, Maryland, and 1 male and 1 female were collected at light in May at Chouteau, Oklahoma.

Bionomics. — Members of this species have been taken in January and from April to December but most have been taken in May, June, and July. Lindroth (1968) reported that in Canada *ovularis* has been "Found only on the N shore of L. Erie, mainly in drift material, probably as a straggler from the south."

As discussed under the species *dulcicollis*, I have collected *ovularis* in association with *dulcicollis* and *harpaloides* in a pasture 2.7 mi. W. of Millington, Tennessee. During the afternoon of July 3, 1971, T. and L. Erwin and I collected 1 female *ovularis* by digging up herbs and grasses on the edge of a grassy field 4.1 mi. W. of Paris, Virginia. The collecting site was located on a slight slope with well leached soil, scattered grass, and weeds and was exposed to sun from approximately mid-morning to late afternoon. Several specimens of *rusticus* were also taken in this site by digging up plants near the edge of the grassy field. The grassy field had a dense cover of grasses and weeds of approximately 1 to 2 feet height, and no *Gynandrotarsus* were found in it.

Label data indicate specimens have been taken as follows: 1 female on ground; 3 males, 1 female under boards in pasture; and 1 female from nest of *Microtus ochrogaster* at Urbana,

Illinois; 2 males, 2 females from commercial orchard at Kearneysville, West Virginia; 1 female in ocean drift at Ocean Beach, Fire Island, New York; and 1 female under log near the Patuxent River, Maryland.

Distribution and material examined (277 specimens). This species is primarily centered in the plains area of east central United States but is known from as far south as Texas and Mississippi, as far north as southern Canada, and as far east as New Jersey and New York (Fig. 163).

28 subgenus *Anadaptus* Casey
(Figs. 176, 188, 189, 190, 206, 207)

Anadaptus Casey, 1914: 203. [TYPE SPECIES: *Anisodactylus discoideus* Dejean, 1831, designated by Lindroth (1968)].

Description. — Body length 8.3 to 13.2 mm. Body convex and subcylindrical, somewhat stouter in *discoideus*.

Color. Various.

Head. Labral apex slightly to strongly emarginate medially. Clypeus with apex straight to slightly emarginate medially; 1 to 4 setigerous punctures at each outer distal angle depending on species. Frons with frontal fovea (if not obscured by punctures) somewhat linear and with clypeo-ocular prolongation; with or without median single or double rufous spot; microsculpture of most specimens obsolete medially and elsewhere of isodiametric mesh. Mentum without tooth or in some specimens with vestigial tooth.

Thorax. Pronotum somewhat cordiform, sinuate behind in most species; posterior angle acute to slightly obtuse, broadly rounded in *rotundangulus*; lateral depression various; lateral bead complete; apical and basal beads present laterally and in most specimens also medially; microsculpture of most specimens obsolete medially and elsewhere of isodiametric mesh. Prosternum completely pubescent in *viridescens*, with glabrous median area in other species. Proepisternum glabrous except for occasional fine short setae at anterior end. Mesosternum pubescent. Mesepisternum and mesepimeron pubescent, except in some examples of *discoideus*. Metasternum and metepisternum of most specimens with some pubescence.

Legs. Foretibia with distal portion laterally expanded; apical spur of most specimens angulate near base but extremely varied, grading (Figs. 188, 189, 190) within individual species from relatively slender (Fig. 188) to (few specimens) subtrifid (Fig. 190). Hind tarsus stout and short; segment I shorter than II + III. Dorsum of all tarsi sparsely pubescent except in some *discoideus*; last segment with 3 to 6 pairs of ventral setae. Fore- and mid-tarsus of ♂ with apex of segment I in some specimens and all of segments II to IV in all specimens laterally expanded and spongy pubescent beneath.

Elytron. Humerus with small tooth in some specimens; intervals flat to convex; pubescence and punctuation restricted to sides and apex or expanded over entire elytron, concentrated on even intervals when so expanded; microsculpture of isodiametric mesh, but more prominent and subgranulate in some ♀♀, and nearly obsolete in ♂♂ of *discoideus*.

Abdomen. Sterna with pubescence varied according to species; sternum VI of ♂ with 1 or 2 pairs of ambulatory setae. Apex of tergum VIII of ♀ rounded.

Male genitalia. Median lobe (Figs. 206, 207) with "button"-like apical disc; membranous area long, extended nearly to basal bulb in most specimens. Internal sac without armature.

Female genitalia. Valvifer moderately sclerotized and slightly convex in ventral view; distal portion with setae of various numbers and sizes; shape greatly varied, changing from lobed to non-lobed within several species as presently defined.

Discussion. — Casey (1914) proposed *Anadaptus* as a separate genus apparently on the

basis of the narrow, convex body form and cordiform pronotum of its species. However, body form in *discoideus* is certainly as stout as that in other subgenera of *Anisodactylus*, and cordiform pronota occur in other subgenera. Lindroth (1968) correctly treated *Anadaptus* as a subgenus of *Anisodactylus*.

Casey (1914) produced a key to the species which he recognized as *Anadaptus*, but like most of his keys, it was difficult to use and excessively split species. Lindroth (1968) revised the Canadian species and some of the United States ones and provided a key to all the Canadian and many of the United States forms; he has suggested (personal communication) that the more southern forms need additional work.

The species *rotundangulus* was originally described as an *Anisodactylus* by Bates (1878a) and also treated as a member of this genus in his classic work (1882) on the Carabidae of Central America. Csiki (1932) listed the species as a member of *Anisotarsus*, probably as an unintentional error since he did not follow his usual practice of citing in parentheses the original genus in which the species was proposed. Van Emden (1953) did not mention the species in his revision of *Anisotarsus*. The species *rotundangulus* is a member of the genus *Anisodactylus* and of the subgenus *Anadaptus*, and shares the following characters with other members of *Anadaptus*: mentum and submentum completely fused (as in all species of the genus *Anisodactylus* but in no members of *Anisotarsus*); hindtarsus short and with segment I shorter than II + III; dorsum of all tarsi sparsely pubescent; apex of female abdominal tergum VIII rounded; median lobe with prominent "button"-like apical disc; internal sac without armature; and valvifer moderately sclerotized, with setae distally and lobed as in several other species within the subgenus.

The species *rotundangulus* is presently known only from central Mexico. The other 7 species are found in Canada and the United States and are: *alternans* LeConte, 1849; *discoideus* Dejean, 1831; *nivalis* Horn, 1880; *porosus* Motschulsky, 1845; *pitychrous* LeConte, 1861; *sanctaerucris* (Fabricius), 1798; and *viridescens* LeConte, 1861.

29 subgenus *Spongopus* LeConte
(Figs. 179, 185, 230)

Spongopus LeConte, 1848: 377. [TYPE SPECIES: *Spongopus verticalis* LeConte, 1848, by monotypy].

Description. — Body length 12.8 to 14.0 mm. Body with short, cordate prothorax and long, parallel sided elytra.

Color. Body black or dark piceous on dorsum; frons with large rufous spot; venter and appendages lighter than dorsum.

Head. Mandible prolonged with pointed, arcuate apex; dorsal surface striate. Labral apex strongly emarginate medially. Clypeal apex straight in most specimens. Frons with fovea small, elliptical, deep pit continued posteriorly toward eye as shallow clypeo-ocular prolongation; microsculpture of isodiametric mesh, obsolete medially in most specimens. Mentum with or without tooth. Paraglossa (Fig. 179) of most specimens slightly longer than ligula and with apices bent towards ligula.

Thorax. Pronotum (Fig. 185) short, broad, cordate (often more so than in Fig. 185); side straight or slightly sinuate before obtuse but prominent posterior angle; disc with scattered, generally fine punctures. Prosternum pubescent. Proepisternum, mesosternum, mesepisternum, mesepimeron, metasternum, and metepisternum pubescent.

Legs. Foretibia with distal portion slightly expanded laterally; apical spur stout, slightly swollen at base in some specimens. Hindfemur with 2 long setae and several shorter ones on posterior margin. Hindtarsus with segment I slightly shorter than II + III. Last segment of

all tarsi with 4 to 5 pairs of ventral setae. Fore- and midtarsi of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals finely, irregularly covered with non-setigerous punctures; outer 2 or 3 intervals pubescent; interval III in most specimens with dorsal setigerous puncture adjacent to stria II about 1/3 distance from apex.

Abdomen. Sterna with irregular pubescence, such pubescence denser and more regular anteriorly on abdomen; sternum VI of ♂ with 1 pair of ambulatory setae. Tergum VIII of ♀ with rounded apex.

Male genitalia. Median lobe stout, slightly swollen medially; lacking apical disc; membranous area of dorsum various, proximal boundaries may be difficult to distinguish, in some specimens with an elongate narrow extension reaching area of basal bulb; field of scale-like spines (arising from internal sac) may project from ostium. Everted internal sac with irregular mushroom like shape and with gonopore situated on side; with 2 fields of armature, basal one (which in most specimens projects through ostium when sac in repose) consisting of scale like spines, apical field of elongate spines.

Female genitalia. Valvifer (Fig. 230) moderately sclerotized, slightly convex; lateral margin membranous and irregular in some specimens; with 1 seta on distal mesal margin in most specimens. Stylus of most specimens with basal segment bearing 1 or 2 very small setae on distal lateral margin.

Discussion. — This subgenus contains only the species *verticalis* LeConte, 1848 found in southeastern Canada and eastern United States.

Spongopus has been treated by most workers, although often with reservations, as an independent genus. However, Lindroth (1968) showed that it is best regarded as a subgenus of *Anisodactylus*. He pointed out that the single character of any value that might justify keeping *Spongopus* as a separate genus is the mental tooth described by many authors, but further noted that this tooth actually varies from absent to well developed (though always more obtuse and less prominent than in *Anisotarsus*). I have confirmed this observation and also noted that in other species of *Anisodactylus* the mental tooth varies in the same manner. The general habitus of *Spongopus* is certainly distinctive but does not warrant generic separation. And as noted by Lindroth the elongate, pointed, striate mandibles and the elongate labrum, which have also been used to justify separate generic status, may be adaptations to a predatory mode of living.

30 subgenus *Aplocentrus* LeConte
(Figs. 203, 223)

Aplocentrus LeConte, 1848: 385. [(*Haplocentrus* auct.) TYPE SPECIES: *Harpalus caenus* Say, 1823, designated by Lindroth (1968)].

Description. — Body length 7.8 to 11.5 mm. Body broad and *Amara*-like.

Color. Body piceous to black. Dorsum with metallic greenish, aeneous, bronze, or bluish tinges.

Head. Labral apex moderately to strongly emarginate medially. Clypeal apex straight to slightly emarginate medially. Frontal fovea bearing prominent clypeo-ocular prolongation. Mentum without tooth in most specimens. Paraglossa slightly longer than ligula.

Thorax. Pronotum relatively broad; lateral depression prominent; microsculpture of isodiametric mesh. Prosternum densely pubescent in *amaroides*, more sparsely so and often with median glabrous area in *caenus*. Proepisternum of many specimens pubescent anteriorly, glabrous posteriorly. Remainder of venter pubescent in most *amaroides* and glabrous or nearly glabrous in *caenus*.

Legs. Foretibia with distal portion moderately expanded laterally; apex emarginate, outer angle of emargination prominent in most *amaroides* and more rounded in most *caenus*; apical spur prominently swollen or somewhat angulate near base in *amaroides*, not or only slightly swollen near base in *caenus*. Hindfemur with various numbers of long setae on posterior margin. Dorsum of all tarsi glabrous or pubescent; last segment with 4 to 5 pairs of ventral setae. Hindtarsus with first segment longer in most *caenus* and shorter in most *amaroides* than II + III. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with apex of segment I in some specimens and all of segments II to IV in all specimens laterally expanded and spongy pubescent beneath.

Elytron. Intervals generally flat; interval III with 1 dorsal puncture near apical 1/3.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Tergum VIII of ♀ with triangular apex (Fig. 203).

Male genitalia. Median lobe with apex in dorsal view slightly deflected to right in *caenus*.

Female genitalia. Valvifer (Fig. 223) lightly sclerotized, thin and platelike, somewhat triangular; distal margin with 1 to 4 setae. Stylus with basal segment bearing 2 or 3 setae on distal lateral margin.

Discussion. — *Aplocentrus* has been given different status and regarded as including different species by various authors. In his fine work on North American *Anisodactylus* Lindroth (1968) correctly regarded *Aplocentrus* as a subgenus of that genus. However, Lindroth placed *caenus* and *laetus* in *Aplocentrus* while placing *amaroides* in a separate informal group of apparently equal weight to a subgenus. The species *laetus* warrants separate subgeneric status, and I place it in the new subgenus *Pseudaplocentrus* for reasons discussed under that taxon.

Lindroth placed *amaroides* in a separate group from *caenus* because he felt the former species had: hind tarsus with segment I shorter than II + III and hardly exceeding elongate apical spur of hindtibia; foretibial apex more strongly emarginate and with outer angle of emargination not rounded; and apical spur of foretibia basally swollen. In contrast, *caenus* was reported to have: hind tarsus with segment I as long as II + III and much longer than apical tibial spur; foretibia with outer angle of emargination more rounded; and apical spur of foretibia slender. In samples of 15 specimens of each species, the ratio of the length of the first segment of the hindtarsus divided by the combined lengths of II + III varies from 0.75 to 0.91 in *amaroides* and from 0.86 to 1.3 in *caenus*; while the ratio of the length of the first segment of the hindtarsus divided by the length of the hindtibial apical spur varies from 0.856 to 1.07 in *amaroides* and from 1.0 to 1.4 in *caenus*. The strength of the emargination and prominence of the outer angle of the foretibial apex vary considerably within each of the species and are not stable enough for reliable separation. The apical spur of the foretibia does seem to be swollen or even slightly angulate near the base in all *amaroides*, but the spur in *caenus* varies somewhat more and in some specimens is slightly swollen near the base.

The species *amaroides* and *caenus* are in fact closely related by their similar valvifers, similar apex on female eighth abdominal tergum, and presence of setae on basal segment of stylus. The subgenus *Aplocentrus*, as defined here, then includes 2 species: *amaroides* LeConte, 1851 from western Canada and western United States; and *caenus* (Say), 1823 from eastern Canada and eastern United States. These species are closely related on morphological grounds, exhibit spatial vicariance, and in my opinion are sister species.

31 subgenus *Pseudaplocentrus* NEW SUBGENUS
 (Figs. 202, 225)

TYPE SPECIES: *Anisodactylus laetus* Dejean, 1829, by present designation and monotypy.

Description. — Body length 8.0 to 9.0 mm. Body relatively narrow.

Color. Body piceous to black. Dorsum with metallic green or aeneous tinge. Appendages of most specimens lighter than body.

Head. Frontal fovea bearing clypeo-ocular prolongation. Eye very large and strongly protruding. Mentum without tooth in most specimens. Paraglossa membranous, slightly longer than ligula.

Thorax. Pronotum with wide flattened lateral depression abruptly set off from disc by prominent inflexion of integument except inflexion absent in basal 1/5 though flattened lateral depression still apparent there; flattened lateral depression translucent in many specimens; lateral, apical and basal beads present.

Legs. Hindfemur with 2 to 4 long setae on posterior margin. Hind tarsus with segment I shorter than II + III. Fore- and midtarsi of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals convex; striae extremely prominent, simirectangular in cross section; interval III with 1 dorsal setigerous puncture approximately 1/2 distance from apex.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Tergum VIII of ♀ with rounded apex (Fig. 202).

Male genitalia. Median lobe with ventral surface somewhat serrate in lateral view.

Female genitalia. Valvifer (Fig. 225) thick, heavily sclerotized, slightly convex in ventral view; without setae; distal portion with prominent ridge from which surface sharply slopes towards apex and sides. Stylus with basal segment bearing 2 or 3 setae on distal lateral margin.

Discussion. — This subgenus contains only the species *laetus* Dejean, 1829 found in the eastern United States. Various authors have included this species in *Aplocentrus* or simply placed it in *Anisodactylus* without subgeneric assignment. Actually, *laetus* warrants separate subgeneric status because the following apomorphic features are absent in other species of *Anisodactylus*: eye large and protruding; pronotum with lateral depression as described above; and elytral striae extremely prominent and simirectangular in cross section.

32 genus *Geopinus* LeConte
 (Figs. 195, 196, 200, 226, 236)

Geopinus LeConte, 1848: 271. [TYPE SPECIES: *Daptus incrassatus* Dejean, 1829, by monotypy].

Description. — Body length 13 to 17.0 mm. Body rather stout, head with broad neck, and prothorax small and narrow.

Color. Pale rufotestaceous, pronotum of most specimens with darker median area, and elytron with at least inner striae darker and inner intervals somewhat infuscated.

Head. Mandible stout, strongly arcuate; apex deeply striate. Labral apex moderately emarginate medially. Gena in front of eye with broad sulcus receiving first antennal segment when in repose. Eye small. Frons with fovea small, elliptical; microsculpture obsolescent. Mentum without tooth. Mentum and submentum completely fused. Ligula strongly expanded laterally at apex. Paraglossa slightly shorter than ligula.

Thorax. Pronotum narrow, only slightly wider than head; lateral bead complete but fine; apical and basal beads present; microsculpture obsolescent.

Legs. Foretibia (Fig. 195) with apical portion strongly expanded laterally; with large excavate dilation at external apex; apical spur slender or slightly swollen medially. Distal portion of mid- and hindtibia strongly expanded laterally. Hindfemur of most specimens with more than 10 long setae on posterior margin. Hindtibia with spatulate apical spur. Hindtarsus short, strongly tapering distally (Fig. 196); segment I shorter than II + III. All tarsi with segment I to IV bearing numerous prominent lateral and latero-ventral spines; segment V with 2 to 5 pairs of ventral setae; dorsum of all segments glabrous. Foretarsus of ♂ with segments II to IV moderately expanded laterally and sparsely spongy pubescent beneath. Midtarsus of ♂ unmodified.

Elytron. Scutellar stria lacking ocellate puncture at base; humerus rounded; without dorsal punctures; microsculpture of weak fine isodiametric mesh along side, base, and apex, obsolescent elsewhere.

Abdomen. Sterna with varied short pubescence (absent on sternum VI in most specimens) and varied numbers of long ambulatory setae. Tergum VIII of ♀ with very broadly rounded apex (Fig. 200).

Male genitalia. Median lobe with ostium in median position; lacking apical disc. Internal sac without armature.

Female genitalia. Valvifer (Fig. 226) moderately sclerotized, slightly convex and with numerous distal setae. Stylus (Fig. 236) with basal segment bearing several prominent setae on distal lateral margin; apical segment elongate, with long setae arising close together on distal 1/3 and with several irregularly distributed shorter setae.

Discussion. — This genus contains only the species *incrassatus* (Dejean), 1829 found in the eastern half of the United States and southern Canada. For a long time *Geopinus* was placed in the subtribe Daptini. However, Ball (1960a) pointed out that the males of *Geopinus* do have spongy pubescence on the venter of the foretarsus and a symmetric median lobe and concluded that *Geopinus* could be placed in the subtribe Anisodactylina. Lindroth (1968) agreed and suggested that the antennal sulcus on the head and the modified fore- and midtibia of *Geopinus* are adaptations to its fossorial mode of living. I agree completely with the conclusions of Ball and Lindroth.

33-34 genus *Amphasia* Newman

Amphasia Newman, 1838: 388. [TYPE SPECIES: *Amphasia fulvicollis* Newman, 1838, by monotypy, = *interstitialis* Say, 1823].

Description. — Body length 8.5 to 14.0 mm. Body relatively slender, covered with dense pubescence.

Head. Mentum without tooth. Mentum and submentum completely fused.

Thorax. Pronotum with side evenly rounded; posterior angle broadly rounded; lateral bead complete; apical and basal beads present at least laterally. Prosternum pubescent. Proepisternum of most specimens pubescent anteriorly and glabrous posteriorly. Mesosternum, mesepisternum, mesepimeron, metasternum, metepisternum, and metepimeron pubescent.

Legs. Foretibia with distal portion slightly expanded laterally. Hindtarsus slender; segment I slightly shorter to slightly longer than II + III. Dorsum of all tarsi pubescent; last segment with 4 to 6 pairs of ventral setae. Foretarsus of ♂ with segments I to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Entire surface with dense uniform pubescence.

Hind wing. Full and apparently functional.

Abdomen. Sterna covered with pubescence; sternum VI of ♂ with 1 pair of ambulatory

setae. Tergum VIII of ♀ with obtusely pointed apex (Fig. 201).

Female genitalia. Stylus dilated laterally, modified as described under subgenera.

Discussion. — *Amphasia* includes 2 subgenera: the nominate one with the single species *interstitialis* (Say), 1823, and *Pseudamphasia* with the single species *sericeus* (Harris), 1828. Both species are found in southeastern Canada and eastern United States. The close phylogenetic relationship of *Amphasia* and *Pseudamphasia* is shown by their synapomorphic character states of: elytron densely and uniformly pubescent; and stylus modified. The stylus in *Amphasia* is strongly dilated laterally and the apical segment has a serrate lateral margin with stout spines arising between the serrations (Fig. 234). The stylus in *Pseudamphasia* is less strongly modified being moderately dilated laterally and having on the apical segment (when not worn) a finely serrate lateral margin with very small spines arising from indentations between the serrations (Fig. 233). The elytral pubescence and modified styli, together with other characters discussed in the section on phylogeny of the genera and subgenera of Anisodactylina, suggest that *Amphasia* and *Pseudamphasia* are closely related sister groups.

While closely related, *Amphasia* and *Pseudamphasia* differ in enough characters normally conservative for groups of Anisodactylina to warrant separate subgeneric status: the stylus of *Pseudamphasia* is less derived than that of *Amphasia*; the valvifer in *Amphasia* (Fig. 229) is not vestigial while that of *Pseudamphasia* (Fig. 233) is; and the ligula of *Pseudamphasia* (Fig. 177) is expanded at the apex while that of *Amphasia* (Fig. 178) is not. Other characters less conservative for groups of Anisodactylina (and therefore of less subgeneric significance) separate the 2 subgenera: the frontal fovea of *Pseudamphasia* is large and shallow while that of most specimens of *Amphasia* is small and relatively deeper; and in *Pseudamphasia* the pronotal apex is less deeply emarginate, the elytral humerus more angulate, the body color different, and the setigerous punctures of the pronotum and elytron finer than in *Amphasia*.

33 subgenus *Pseudamphasia* Casey
(Figs. 177, 233)

Pseudamphasia Casey, 1914: 195. [TYPE SPECIES: *Harpalus sericeus* Harris, 1828, by monotypy].

Description. — Body length 8.8 to 11.0 mm.

Color. Dorsum and venter piceous to black; frons with or without median rufous spot. Legs rufotestaceous to rufopiceous, femora darker in many specimens.

Head. Frons with fovea irregular, large, shallow, without clypeo-ocular prolongation; microsculpture of very prominent isodiametric mesh. Ligula with apex expanded laterally (Fig. 177); margin of apex with small tubercle medially in many specimens. Paraglossa subequal in length to ligula, narrowly rounded at apex (Fig. 177).

Thorax. Pronotum with microsculpture of prominent isodiametric mesh.

Elytron. Surface with dense, uniform pubescence (finer however than in *Amphasia*); humerus slightly angulate, without tooth, microsculpture of granulate slightly transversely stretched isodiametric mesh, more prominent in ♀; without iridescence.

Male genitalia. Median lobe with apex bent ventrad; ventral surface with prominent longitudinal striae. Internal sac with complex armature.

Female genitalia. Valvifer (Fig. 233) small, flat, vestigial; membranous except near lateral and mesal articulations; situated at base of stylus (Fig. 233) and difficult to find. Stylus (Fig. 233) moderately dilated laterally; lateral margin of apical segment finely serrate and with very small spines arising from indentations between fine serrations (serrations and spines much finer than those in *Amphasia*).

34 subgenus *Amphasia* Newman
(Figs. 178, 201, 229, 234)

Amphasia Newman, 1838: 388. [TYPE SPECIES: *Amphasia fulvicollis* Newman, 1838, by monotypy, = *interstitialis* Say, 1823].

Description. — Body length 8.5 to 10.2 mm.

Color. Dorsum with head and pronotum testaceous to rufotestaceous; elytron piceous and strongly iridescent. Venter various.

Head. Frons with fovea small, somewhat irregular in shape, in many specimens vaguely crescent shaped with both ends medially directed, in some specimens Y shaped with 2 forks directed posteriorly; microsculpture of isodiametric mesh, more prominent in ♀, obsolescent medially in many ♂♂. Ligula slender, not expanded at apex (Fig. 178). Paraglossa slightly longer than ligula, broad and obtuse at apex.

Thorax. Pronotum with microsculpture obsolescent or consisting of fine lines.

Elytron. Surface with dense, uniform pubescence; humerus rounded, without tooth; microsculpture of extremely dense, fine transverse lines, causing strong iridescence.

Male genitalia. Median lobe with apex bent sharply ventrad; sclerotized virga present on both sides of ostium. Everted internal sac with median field of prominent enlarged scales.

Female genitalia. Valvifer (Fig. 229) flattened, lightly sclerotized, with 2 to 5 distal setae. Stylus (Fig. 234) strongly dilated laterally; lateral margin of apical segment serrate and with short stout spines arising between serrations from dorsal side.

35 genus *Gynandromorphus* Dejean
(Figs. 197, 231)

Gynandromorphus Dejean, 1829: 186. [TYPE SPECIES: *Carabus etruscus* Ouensel, 1806: 212, by monotypy].

Morphogynandrus Carret, 1905: 122. [TYPE SPECIES: *Gynandromorphus peyroni* Carret, 1905, by monotypy].

Description. — Body length 10 to 11 mm. Body densely pubescent, form as in *Diachromus*.

Color. Dorsum tricolored; head and pronotum black; base of elytron rufotestaceous; apex of elytron violaceous brown. Venter black. Legs testaceous to rufotestaceous.

Head. Frontal fovea obsolescent, obscured by setigerous punctures. Mentum with prominent tooth. Mentum and submentum completely fused. Ligula very strongly expanded laterally at apex. Paraglossa slightly shorter than ligula.

Thorax. Pronotum cordate; lateral bead complete; apical bead present laterally; basal bead present at least laterally.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur trifid. Hindtarsus with segment I shorter than II + III. Dorsum of all tarsi pubescent. Foretarsus of ♂ with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Foretarsus of ♀ with segment I enlarged and laterally expanded, remaining segments unmodified. Midtarsus of ♂ with segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals moderately to densely pubescent; interval III without discernible dorsal setigerous puncture.

Abdomen. Sternum VI of ♂ with 1 or 2 pairs of ambulatory setae depending on species. Tergum VIII of ♀ with strongly angulate apex (Fig. 197).

Male genitalia. Median lobe of some specimens with distal portion deflected to the right; lacking apical disc.

Female genitalia. Valvifer (Fig. 231) moderately sclerotized, slightly convex; mesal margin somewhat membranous and indistinct; lateral margin distinct but with membranous lobe; distal portion with several prominent setae. Stylus with basal segment bearing 1 or 2 very small indistinct setae on lateral distal margin.

Discussion. — This genus contains 2 species: *etruscus* (Quensel), 1806 found in southern and middle Europe; and *peyroni* Carret, 1905 found in Syria and the Transcaspian. Carret (1905) placed his new species in a new subgenus, *Morphogynandrus*, but subsequent authors have agreed that the characters cited by him are neither important nor stable enough to warrant separate subgeneric status for *peyroni*.

36 genus *Diachromus* Erichson
(Figs. 204, 228)

Diachromus Erichson, 1837: 43. [TYPE SPECIES: *Carabus germanus* Linnaeus, 1758, by monotypy].

Description. — Body length 8 to 10 mm. Body convex, somewhat slender, pubescent.

Color. Dorsum tricolored; head and base of elytron rufotestaceous; pronotum black, apex of elytron violaceous or bluish brown. Venter black.

Head. Frontal fovea obsolescent, obscured by setigerous punctures. Mentum with prominent tooth. Mentum and submentum completely fused. Ligula strongly expanded laterally at apex. Paraglossa approximately equal in length to ligula.

Thorax. Pronotum cordate; with seta located near middle of each lateral margin and additional seta situated by posterior angle; lateral bead complete; apical bead present only laterally; basal bead present but in many specimens obsolescent medially.

Legs. Foretibia with distal portion moderately expanded laterally; apical spur laterally expanded and somewhat spatulate. Hindtarsus with segment I shorter than II + III. Fore- and midtarsus of ♂ with apex of segment I (only extreme apical margin in midtarsus) and all of segments II to IV laterally expanded and spongy pubescent beneath.

Elytron. Intervals with dense, erect pubescence; interval III with discernible dorsal setigerous puncture near apical 1/4 in most specimens.

Abdomen. Sternum VI of ♂ with 2 pairs of ambulatory setae. Tergum VIII of ♀ with obtusely rounded apex (Fig. 204).

Male genitalia. Median lobe with median portion swollen in dorsal view; lacking apical disc.

Female genitalia. Valvifer (Fig. 228) moderately sclerotized; distal portion with several short setae. Stylus with basal segment bearing 1 or 2 short setae on apical lateral margin.

Discussion. — This genus contains only the species *germanus* (Linnaeus), 1758 found in England, southern Europe and around the Mediterranean. It is distinguished from all other Palearctic Anisodactylines by the additional seta present near the pronotal posterior angle.

37 genus *Dicheirus* Mannerheim

Dicheirus Mannerheim, 1843: 211. [TYPE SPECIES: *Harpalus dilatatus* Dejean, 1829, designated by Noonan (1968)].

Description. — Body length 5.3 to 14.5 mm. Body covered with setigerous punctures.

Color. Rufous to black depending on body part and on species; without metallic tinge.

Head. Clypeus with 1 to 4 setigerous punctures at each outer distal angle. Frontal fovea obsolescent. Mentum with or without tooth. Mentum and submentum completely fused. Ligula strongly expanded laterally at apex. Paraglossa slightly longer than ligula; with very

fine, short hairs on sides, apex, and dorsum (evident at magnifications of 120X or more).

Thorax. Pronotum with lateral bead complete; apical bead absent; basal bead present but in many specimens interrupted medially.

Legs. Foretibia with distal portion strongly expanded laterally; apical spur strongly trifid. Hindtarsus with segment I shorter than II + III. Dorsum of all tarsi with sparse to dense pubescence. Foretarsus of ♂ (except some specimens of *dilatatus angulatus*) with apex of segment I and all of segments II to IV laterally expanded and spongy pubescent beneath. Midtarsus of ♂ with or without some segments laterally expanded and spongy pubescent beneath.

Elytron. Intervals II to VII, II to VIII, or II to IX, depending on species, with 2 rows of setigerous punctures; outer intervals with irregular row(s) of setigerous punctures; interval III without apparent dorsal setigerous puncture.

Hind wing. Full and apparently functional or vestigial depending on species.

Abdomen. Sternum VI of ♂ with 1 or 2 pairs of ambulatory setae in most specimens. Tergum VIII of ♀ various.

Male genitalia. Median lobe without apical disc; membranous area of dorsum elongate and extended nearly to basal bulb in all species except *obtusus*; entire shaft twisted in *piceus*, not twisted in other species. Internal sac without armature.

Female genitalia. Valvifer various according to species. Stylus with basal segment bearing 2 to 4 prominent long setae on apical lateral margin; apical segment in all species except *obtusus* with several setae at base.

Discussion. — The 5 species of this genus, all found in the western United States or southwestern Canada, are: *brunneus* (Dejean), 1829; *dilatatus* (Dejean), 1829; *obtusus* LeConte, 1851; *piceus* (Menetries), 1844; and *strenuus* (Horn), 1868. Noonan (1968) revised the genus and provided a key to the species, and Lindroth (1968) keyed out the northern forms. *Dicheirus* has been placed in *Anisodactylus* by some past authors but warrants separate status due to the total absence of an apical bead on the pronotum (Lindroth, 1968) and the densely pubescent elytra.

PHYLOGENY

Introduction

Hennig (1966) provided principles for reconstructing phylogenies of extant organisms, leading to renewed interest in methods for elucidating phylogenies. Four workers have produced major papers discussing, variously modifying, and utilizing Hennig's principles in reconstructing phylogenies of insect groups: Brundin (1966) on midges of the South Hemisphere; Erwin (1970) on species of *Brachinus* (Coleoptera: Carabidae); Donald Robert Whitehead (1972) on species of *Schizogenius* (Coleoptera: Carabidae); and Griffiths (1971) on Cyclorrhapha (Diptera).

Seven workers have published important papers on theoretical aspects of phylogenetic principles. Hull (1970) and Mayr (1969) reviewed the principles of Hennig and the broadened phylogenetic principles enunciated by Brundin (1966) and discussed other systems for constructing classifications. Darlington (1970) pointed out practical problems concerning the principles of Hennig and Brundin. In turn, Nelson (1971a) defended Hennig and Brundin's ideas and offered arguments for accepting dichotomous evolution. Darlington (1972) replied to Nelson's comments and asked for clarification of Hennig and Brundin's principles. Brundin (1972) defended his and Hennig's ideas and criticized Darlington's (1970) paper. And Ashlock (1971), Colless (1972), and Nelson (1971b) dealt with definitions of monophyly, paraphyly, and polyphyly.

Phylogenetic Methods

From the many ideas and models discussed by the above authors I selected the following methodological principles for constructing Anisodactyline phylogenies: (1) assumption of dichotomous cleavage of each ancestral taxon to produce 2 sister taxa; (2) determination of relationships by synapomorphy; (3) clarification of relationships by chorology.

Darlington (1970) pointed out that dichotomous cleavage has not been proven for the evolution of species, is in fact unlikely, and is an oversimplification of what actually occurs in nature. These points may well be true. However, available data may not clearly indicate whether a species or higher taxon simultaneously split into 2, 3, 4 or whatever number of descendants. Therefore, I believe dichotomous cleavage, used as a methodological model, is a legitimate assumption that allows reconstructing an orderly phylogeny in accord with the principle of parsimony.

Hennig (1966) and Brundin (1966) asserted that sister taxa should be given equal rank. This stems in part from their belief that dichotomous evolution is the actual way in which evolution proceeds rather than being simply a convenient model by which to construct orderly phylogenies. Giving equal rank to sister taxa would lead to excessive splitting of groups and require additional supra-specific categories. Therefore, I have not always given equal rank to sister taxa in this paper.

The logical first step in reconstructing a phylogeny of extant organisms is to determine which of them are most closely related on the basis of synapomorphy and chorology. Most extant taxa can be grouped into pairs (sister taxa) the members of which are more closely related to each other than to any other extant taxon.

Some taxa may appear to lack sister taxa because: (1) the sister taxa are extant but not yet collected; (2) the sister taxa are extinct; (3) three or more taxa are equally related to each other due to simultaneous evolution from the same ancestor. The first two possibilities can be evaluated by a specialist familiar with how well the group in question has been collected and how common extinctions appear to be in the group. The third possibility can be evaluated by determining if 3 or more taxa are as closely related to one another as any 2 of them are to each other. If 3 or more taxa do indeed seem so related, then the phylogeny should be drawn to reflect this, with an ancestral taxon shown as simultaneously dividing into 3 or more taxa. Unpaired taxa which have resulted from the first 3 possibilities should be connected to the phylogeny by dotted lines, and their most probable relationship to paired or sister taxa in the group discussed.

Determination of plesiomorphic and apomorphic character states is essential for elucidation of sister taxa. Plesiomorphic character states are those which evolved in a relatively early ancestor of a group of taxa. The plesiomorphic character states may be retained by various extant taxa and therefore may characterize both closely and distantly related taxa. Apomorphic character states are those which evolved in a more recent ancestor of a group of taxa and consequently are more likely to be restricted to a single taxon or to a single monophyletic group of taxa. Therefore, the use of apomorphic character states as indicators of relationship is less likely to result in distantly related forms being mistakenly treated as closely related.

When fossils are scanty or absent (as in Carabidae), the best method of distinguishing apomorphic character states from plesiomorphic ones is to analyze morphoclines (transformation series) as suggested by Maslin (1952). If such morphoclines are not found, one must assume that character states widespread among diverse groups are plesiomorphic while those restricted to only a few groups are apomorphic or less likely are relictual. The latter possibility can be evaluated by a worker familiar with the group in question. Lastly, in some instances character states may correlate with other character states whose value is already

known.

The chorological method may help in elucidating relationships by examining extant distribution patterns to determine probable evolutionary histories. Also used are data from such topics as: past floras and faunas; past climates; and past continental drift. Data on past floras, faunas, and climates help in elucidating relationships among species, and together with data on past continental drift may help in determining relationships among supraspecific taxa.

Forms regarded as "sister" taxa may actually not have evolved from an immediate common ancestor but rather be the sole survivors of once extensive sister groups of taxa. Such a hypothetical instance is illustrated in Fig. 244 in which "G", "I" and "C" are the only extant forms of a lineage. The taxa "G" and "I" are the survivors of the sister groups "F", "G" and "H", "I" and share several apomorphic character states which evolved in the extinct taxon "B". A worker reconstructing the phylogeny of "G", "I", and "C" might very likely draw the reconstructed phylogeny as in Fig. 245 thus treating "G" and "I" as sister taxa and as older than they are. A reconstructed phylogeny can only indicate the most probable maximum age of a taxon. Therefore, it often is not correct to determine the age of a taxon by noting where it branches off from the main part of a phylogenetic diagram.

Phylogeny and Chorology

Because several lineages within the subtribe Anisodactylina have no apparent synapomorphies, I used chorological data in assembling the phylogeny. Postulated past movements of continents are especially useful in determining the sequence of development of various lineages and supra-specific taxa of the subtribe Anisodactylina whose origin I presume was in late Jurassic or very early Cretaceous. My primary reference for past positions of continents was Dietz and Holden (1970), the only synthesis I found with clear maps of past positions of all continents. Other sources consulted to confirm (or sometimes slightly modify) conclusions by Dietz and Holden were: Smith and Hallam (1970); Malfait and Dinkleman (1972), and Morgan et al (1969).

Many previous biogeographers who worked primarily with land vertebrates have felt either: that distribution patterns disproved or at least did not suggest continental drift (Matthew, 1915; Darlington, 1957; Simpson, 1962); or that such drift was limited (Darlington, 1965). The present distribution of continents is such that the Northern Hemisphere contains about twice as much land as does the Southern (Darlington, 1957). And the current arrangement of continents is such that "north of the tropics, there are large areas which are nearly connected; within the tropics, large areas which are separated from each other; and south of the tropics, smaller areas which are very widely separated from each other" (Darlington, 1957, p. 3). Matthew (1915) proposed: that the North temperate Region has been the main center of evolution and dispersal of land vertebrates because of past climatic fluctuations; and that no continental drift or former land bridges were necessary to explain contemporary vertebrate distribution. Darlington (1957; 1959) discussed Matthew's ideas and presented arguments for the Old World Tropics as the main center of land vertebrate evolution and dispersal. The disjunct southern land areas were considered primarily as recipients of a stream of animals evolving in and dispersing from larger northern areas (Darwin, 1856; Darlington, 1957, 1959, and especially 1965).

It has been accepted by many workers that the general pattern of land vertebrate evolution has been evolution of dominant forms in northern areas (whether tropical or temperate) and subsequent spread to other lands such as those of the Southern Hemisphere. Darlington (1957, 1959, 1965) presented the following points in support of a northern origin of land vertebrates. As a general rule, continental faunas are superior to and can displace island ones.

And faunas evolved from large areas can usually supplant or out complete faunas evolved from small areas. Dominant groups are the most likely ones to disperse. The Old World Tropics constitute a large area with favorable climate. The general pattern of evolution of land vertebrates has been evolution of dominant groups in the Old World Tropics and subsequent spread to northern and southern lands.

I agree with Darlington that faunas evolving in large areas can usually supplant those evolving in smaller ones, that dominant forms do show a tendency to evolve in areas with favorable climate, and indeed that the evolution of land vertebrates *may* have taken place primarily in northern areas. However, Fooden (1972) convincingly postulated an origin of mammals on Pangaea and correlated current distributions with past episodes of continental drift. And that some or many land vertebrates *may* have evolved in northern areas does not mean insects must also have done so.

More important, the thesis of evolution in northern areas and flow of dominant animals to disjunct southern lands is dependent on the thesis of permanence of continents. Geologists now agree that continents have not always had their present positions and in fact have moved quite freely over the surface of the earth. Data supplied by many workers including the geologists cited earlier indicate that approximately 200 million years ago all continents were grouped into a single supercontinent, "Pangaea". During much of the Mesozoic, Australia, New Zealand, New Guinea, and Antarctica constituted a single landmass while Africa and South America were also joined. The Australia-Antarctica landmass, the South America-Africa landmass, and India constituted during part of Mesozoic at first a single joined landmass termed "Gondwanaland" and later (except for India) were closely associated for a long period of time (Figs. 247, 250).

The existence of a large unit of closely situated or joined landmasses satisfies Darlington's requirement of large land area for evolution of dominant forms. And the past positions of these landmasses suggest favorable climate, thus satisfying Darlington's second criterion. The area-climate-evolution hypothesis of Darlington thus readily permits and even strongly suggests that Gondwanaland may have been an important center of evolution during the Mesozoic. The possible lack of evidence for a Gondwanaland center of origin for many land vertebrates may be due either to evolution of such groups taking place after the continents had nearly or completely reached their present position or to the early fossil record being incomplete. Each group of animals or plants must be carefully examined to determine if its present distribution and fossil record (if present) suggest evolution and dispersal from Gondwanaland. This is especially true of insects!

Several biogeographers have considered continental drift in explaining contemporary distribution of groups of insects. Since I have found the theory of continental drift useful in explaining the present distribution of Anisodactylina, works of 4 of these biogeographers will be discussed to place my own work in a frame of reference. As far as I know, Jeannel was the first biogeographer to employ continental drift theory to explain present distributions of Carabidae. (He also used continental drift theory to explain distributions of other groups of organisms.) Three of his works will be reviewed here. Other works reviewed here are by Ball, Brundin, and Darlington.

In 1938 Jeannel published a revision of Migadopini, a primitive group of Carabidae found in now disjunct areas of the southern hemisphere. Jeannel listed 5 lineages within Migadopini: (1) a primitive Australian-New Zealand lineage comprised of three genera and found in Australia, New Zealand, and the Auckland Islands; (2) an Australian lineage confined to Australia and Tasmania; (3) a derived lineage endemic to New Zealand; (4) a South American lineage containing species with harpaline facies; and (5) a monotypic, phylogenetically isolated Chilean lineage. According to Jeannel, the contemporary distribution of Migadopini

in widely disjunct austral regions is explained by these regions once being grouped together into a single landmass.

In his classic book on southern hemisphere biogeography Darlington (1965) pointed out that: (1) the tribe *Migadopini* contains winged species in both Australia and Chile; (2) the tribe has forms occurring at warm temperate or subtropical localities; (3) existing genera are very diverse, suggesting they are products of a complex ecologic as well as geographic radiation rather than simple spread from an antarctic center and; (4) closest relatives of tribe are probably the north temperate *Elaphrini*. He concluded (p. 37) from these 4 points "that the ancestor of the *Migadopini* was winged, that it may have lived in or dispersed through relatively warm climates, that the history of the tribe has been complex, and that a common ancestor of this tribe and the *Elaphrini* crossed the tropics a long time ago. These details do not disprove an antarctic origin of the *Migadopini* but do suggest other possibilities." Elsewhere (pp. 47-50) Darlington suggested for *Migadopini*, *Broscini*, *Trechini*, and *Bembidion* (latter 3 groups are also Carabidae) an apparent dispersal cycle of: "rise on the large land masses in the Northern Hemisphere, or possibly in the tropics; dispersal southward into southern America and southern Australia by separate routes, and to New Zealand probably from Australia; disappearance of the tropical or tropics-crossing forms, leaving an amphitropical pattern; and finally disappearance from the Northern Hemisphere, leaving survivors on the three main pieces of land in the southern cold-temperate zone. (Other groups might disappear in the Southern Hemisphere and survive only in the Northern.)"

Brundin (1966 pp. 63-64) disputed Darlington's 4 points (and indirectly the suggested dispersal cycle) by stating: (1) presence of winged groups does not disprove past evolution on Gondwanaland nor spread from that landmass; (2) subgroups of *Migadopini* need not be expected to all be adapted to only cold environments; (3) spread from an antarctic center need not be simple; (4) possible relationship to the more apomorphic *Elaphrini* suggests "the apomorphic sister species of the migadopid ancestor migrated northwards and became the ancestor of *Elaphrini*".

Without fossil evidence it will never be possible to *prove* the origin of *Migadopini* nor of other groups of Carabidae. One can only speak in terms of probability. The dispersal cycle suggested by Darlington (1965) may be true for certain possibly more recently evolved groups of Carabidae such as *Bembidion*. However, for older and exclusively austral groups such as *Migadopini* this suggested dispersal cycle requires more assumptions and is therefore less likely than the origin suggested by Jeannel. Further, the dispersal cycle suggested by Darlington assumes "rise on the large land masses in the Northern Hemisphere, or possibly in the tropics"; Gondwanaland was such a landmass, but in the Southern Hemisphere.

In his 1940 revision of *Calosoma* Jeannel provided an extensive discussion of chorology and evolution. He provided maps of past continental drift accepted by him and explained present distribution of *Calosoma* partly on the basis of evolution in and dispersal from Gondwanaland. Certain land arrangements and timings of continental movements postulated by Jeannel are today not accepted by geologists. And the taxonomic work done by Jeannel is weak in some aspects. However, his use of information concerning past continental movements to explain contemporary distribution patterns must be regarded as a pioneering effort.

Jeannel (1942b) produced a biogeography book dealing primarily with the origins and dispersal of insects. Hypotheses about groups were based largely on postulated past continental movements which were illustrated in 8 plates covering the upper Carboniferous to Pliocene. In his eagerness to explain extant insect distributions by continental drift, Jeannel unfortunately formed some taxonomic groups in such a way that they would "fit" continental drift. In his review of the book Darlington (1949) pointed out that it contributed much original information on evolution and on past dispersals of some groups but suffered from

being (p. 345) "a succession of dogmatic statements with no distinction between fact and opinion". Jeannel's failure to consider alternative explanations for extant insect distributions greatly weakens the usefulness of the book. Nevertheless, his work is important to biogeographers since: (1) it is one of the few major works treating insect biogeography in detail; (2) Jeannel did accept continental drift long before many other biogeographers in Europe and North America; (3) information and theories presented in the book should stimulate other biogeographers.

Ball (1956) briefly reviewed the classification and distribution of Broscini (Carabidae) at a time when neither he nor most geologists accepted continental drift. He recognized 3 subtribes: (1) Barypina, restricted to southern South America; (2) Creobina found in southern South America and western Australia; (3) Broscina with center of abundance in the eastern Palearctic but found also in New Zealand, Australia, the Nearctic and the northern fringe of the Oriental Region. Ball concluded that ancestral stocks of the former 2 subtribes possibly arose in the southern hemisphere and reached South America by way of a southern route. He noted that geological data (in 1956) did not support a direct land connection between South America, Antarctica, New Zealand, and Australia. Therefore, he concluded (p. 46) it was impossible to state whether invasion of South America took place "by dispersal from island to island or by way of a direct land connection".

According to Ball (p. 47) the subtribe Broscina most likely "arose in the southeastern Palearctic or in Australia and dispersed from either of these centers possibly by way of what is now the Indo-Australian Archipelago." This is in disagreement with Britton's (1949) suggestion that the tribe Broscini originated on Cretaceous Southern Hemisphere landmasses, probably reached South America by southern land connections, and later spread from there through Africa to Eurasia. Contemporary continental drift theory connects South America, Africa, Australia, New Zealand, New Guinea, and Antarctica during early Mesozoic but does not connect Australia to Asia via the current Indo-Australian Archipelago until Tertiary. Thus, as Britton suggested, dispersal via the Indo-Australian Archipelago may be improbable since Broscines could not have reached Asia via this route early enough to account for the considerable diversification of the Palearctic genera and species.

Ball pointed out that if we knew more about continental drift, we would know more about the most probable dispersal times and routes of Broscines. In view of currently accepted continental drift theory, it seems more probable to me that the ancestor of the subtribe Broscina reached either the South American or African portion of the combined South America-Africa landmass via direct land connections or across narrow water gaps in the Jurassic or early Cretaceous and passed through Africa into the Palearctic. Then the ancestor died out in Africa (and also South America if it ever reached that continent). This postulated dispersal provides adequate time for extensive diversification of genera and species in the Palearctic Region. Later, when the Bering Land Bridge was exposed in the Tertiary, members of the subtribe could have crossed into North America.

Probably the most discussed recent work correlating insect distribution with continental drift is Brundin's 1966 book. In this work Brundin summarized and extended the phylogenetic principles of Hennig (1966) and then employed them in his monograph of the Chironomid subfamilies Podonominae, Aphroteniinae, and the austral Heptagyiae. He also discussed transantarctic relationships of other groups of organisms and explained these relationships in part by continental drift.

Brundin's postulated history of the midges seems possible to me except perhaps that several sister species are found on widely disjunct lands. One or both of the following possibilities may explain this occurrence of sister species on widely disjunct lands: (1) the sister species recognized by Brundin may each actually be the sole survivor of species groups dating

back to the Mesozoic; (2) the sister species may have dispersed via Antarctica during the Tertiary. Dispersal across present water gaps seems unlikely to me because of the danger of desiccation during such dispersal. I am aware that chironomids are frequently taken by aerial nets but know of no studies showing that they are alive at the moment of capture.

Phylogeny of the genera and subgenera of the Anisodactylina.

Table 2 (p. 429) indicates the plesiomorphic and apomorphic states of each character employed in the reconstructed phylogeny of Anisodactylina presented in Figs. 240, 241. Unless otherwise indicated in the text, plesiomorphic and apomorphic states are determined by their distribution among supra-specific taxa of Anisodactylina or other Carabidae.

The extant supra-specific taxa of Anisodactylina can be grouped into 2 main branches: (1) the Notiobioid main branch with the mentum and submentum separated by a complete transverse suture (except *Anisostichus*) and (2) the Anisodactyloid main branch with the mentum and submentum fused only laterally or fused completely. The first group represents the plesiomorphic state in Anisodactylina since as far as I know the mentum and submentum are separated by a complete transverse suture in most other tribes of Carabidae and in all subtribes of Harpalina except the subtribe Bradycellina. Within this latter subtribe the mentum and submentum are fused in species of a few genera but are separated by a complete transverse suture in all other genera. The Anisodactyloid main branch in turn possesses a character state clearly apomorphic within Harpalini and within the subtribe Anisodactylina.

The Australian Region (except for New Guinea which contains 2 species of *Chydaeus* derived from stocks in Asia) lacks members of the Anisodactyloid main branch (Fig. 246) and contains only members of the relatively more plesiomorphic Notiobioid main branch. Moreover, Notiobioids found in the Australian Region are relatively plesiomorphic compared with Notiobioids found in other parts of the world.

The most probable explanation for the absence of apomorphic forms in the Australian Region is that Anisodactylina arose on the combined landmass (hereafter termed Australia-Antarctica) of Australia, Antarctica, New Guinea, and New Zealand, spread to other regions and evolved more apomorphic forms in these other areas.

The Australia-Antarctica landmass was separated from the northern continents by the end of the Triassic (Dietz and Holden, 1970). This might suggest that the ancestor of Anisodactylina arose during the Triassic. However, beetles apparently arose in the Permian (Crowson, 1955), and the Harpalini are moderately apomorphic within the family Carabidae. Therefore, it is more likely that the ancestor of the subtribe arose in Australia-Antarctica during very late Jurassic or early Cretaceous, and then members later crossed the narrow water gap to the combined continents (hereafter termed South America-Africa) of South America and Africa (Figs. 247, 248).

Darlington (1965) pointed out that southern Australia was non glaciated and possibly warmer than now but not tropical from Permian to Tertiary, when it became cooler. New Guinea and the northern edge of Australia (Darlington, 1965) are and probably long have been tropical, and between tropical and south temperate areas of Australia there now is and probably long has been a broad barrier of more or less drier country. Darlington further stated that very few Triassic and Jurassic plants have been so far found on the main part of Antarctica, but a moderately diverse Jurassic flora has been found on the Antarctic Peninsula. Lower Triassic fossil beds along the southwest coast of Antarctica have yielded labyrinthodont amphibians, thecodont reptiles, and therapsid reptiles (Elliot et al, 1970; Fooden, 1972; Kitching et al, 1972). And during Jurassic and early Cretaceous (Dietz and Holden, 1970) the Antarctica portion of Australia-Antarctica was located further north than at present (Fig. 248). The presence of Jurassic fossils on Antarctica and its more northerly

location suggest that this area had a much milder climate than at present. This would permit evolution and migration of Anisodactylina along at least the northern edge of Antarctica. Most of the taxa of Anisodactylina contain species primarily adapted to temperate conditions. And 4 of the 5 presumably oldest groups, (*Allocinopus*, *Triplosarus*, *Hypharpax*, and *Cenogmus*) are primarily centered in temperate areas. Thus, the ancestor of Anisodactylina probably was adapted to temperate or warm temperate conditions.

The endemic New Zealand genus *Allocinopus* does not appear closely related to any other extant groups of the Notiobioid main branch and therefore is connected by a dotted line to the phylogenetic diagram in Fig. 240. Most likely, the ancestor of *Allocinopus* became isolated in New Zealand when this group of islands became separated from Australia and Antarctica. Smith and Hallam (1970) date such separation from middle Jurassic to middle Cretaceous while Dietz and Holden (1970) date it from early Tertiary. The distinctiveness of *Allocinopus*, character variation demonstrated by its species, and the distinctiveness of *Triplosarus* (the other endemic New Zealand genus) suggest separation in the Cretaceous.

The ancestor of *Allocinopus* may have given rise to a group of genera which became extinct except for *Allocinopus*. Or the ancestor may have been a member of a lineage once widespread on Australia and Antarctica. Australia and New Zealand are moderately well collected in terms of Carabidae, and therefore it is unlikely that an extant sister genus will be found. *Allocinopus* appears to be a phylogenetic relict.

The ancestor of Anisodactylina which presumably arose in temperate or warm temperate areas of Australia-Antarctica during late Jurassic or early Cretaceous, soon gave rise to the *Notiobia* and *Cenogmus* branches. The first branch remained essentially unchanged from the ancestral condition, but the second or *Cenogmus* branch gained the apomorphic feature of extra setae on the abdominal sterna. Part of this second branch migrated to the New Zealand portion of Australia-Antarctica, became isolated when New Zealand became separated, and eventually evolved into the endemic genus *Triplosarus*. Smith and Hallam, 1970 stated that such separation probably took place between middle Jurassic and middle Cretaceous, but Dietz and Holden (1970) date separation from early Tertiary. The distinctiveness of *Triplosarus* and of the other endemic New Zealand genus, *Allocinopus*, suggests separation in the Cretaceous. The Australian portion of the *Cenogmus* branch subsequently divided into the *Hypharpax* sub-branch, which ultimately gave rise to the genus *Hypharpax*, and into the *Cenogmus* sub-branch. A member of the *Cenogmus* sub-branch crossed the water gap (Fig. 247) between Australia-Antarctica and South America-Africa. Most likely it never reached the South American part of the landmass but became established in Africa and there evolved into the genus *Crasodactylus*. This genus subsequently spread to India but was displaced from most of tropical Africa by members of the more apomorphic Anisodactyloid main branch.

An alternative possibility for the evolution and dispersal of the *Cenogmus* sub-branch (suggested in part by G. E. Ball, personal communication) is as follows. The genus *Hypharpax* does not possess as many apomorphic character states as do *Crasodactylus* and *Cenogmus*. Acquisition of apomorphic features takes time, and therefore the latter two genera are probably much older than *Hypharpax*. Both *Crasodactylus* and *Cenogmus* evolved on and were at first present over much of Australia-Antarctica (minus the already split off New Zealand). As the landmass split up, both genera remained on the Australian portion and did not cross the water gap to South America or Africa. When the Indo-Australian Archipelago was formed during the Tertiary, *Crasodactylus* used this Archipelago to disperse to tropical Asia. The genus subsequently spread across tropical Asia to Africa and therefore is only a recent arrival there. The more recently evolved genus *Hy-*

pharpax ultimately displaced *Crasodactylus* from Australia, the Indo-Australian Archipelago, and tropical Asia in a manner similar to the "Taxon Cycle" suggested for certain ants by Wilson (1961).

This alternative sequence of evolution and dispersal of the *Cenogmus* sub-branch seems less likely to me than the evolution of *Crasodactylus* in Africa itself. Evolution of *Crasodactylus* in Australia and dispersal across the Indo-Australian Archipelago requires crossing of many water barriers, while evolution of *Crasodactylus* in Africa requires crossing only one water barrier. At the moment there is not sufficient ecological information on the species of *Crasodactylus* and *Hypharpax* to determine if they inhabit similar habitats or if they would have competed with each other in the past if species ranges overlapped. If the assumption is made that *Hypharpax* species did compete with and displace species of *Crasodactylus* in the Tertiary, then at least some of the islands in the Indo-Australian Archipelago might be expected to contain relict populations of *Crasodactylus*. To my knowledge, none do so. And *Crasodactylus* dispersing through tropical Asia to Africa would probably have had to compete with members of the more apomorphic Anisodactyloid branch already in Asia or just dispersing to Asia from western Eurasia and Africa.

These points do not disprove the alternative possibility for the evolution and dispersal of the *Cenogmus* sub-branch. It is possible for groups to cross more than one water barrier. Extinction of groups in areas through which they dispersed is not impossible and in fact was postulated by me earlier in this paper in discussing the dispersal of Broscine carabids. And species of *Crasodactylus* and of the Anisodactyloid main branch may have occupied quite different niches and not been in competition. Nevertheless, the mechanism for evolution and dispersal of the *Cenogmus* sub-branch postulated by me is more parsimonious than the alternative one.

The *Notiobia* branch on Australia-Antarctica was originally characterized by features ancestral for the subtribe. It subsequently split into the *Notiobia* sub-branch which retained ancestral features and into the *Gnathaphanus* sub-branch, which had the apomorphic feature of third elytral interval with few to many dorsal setigerous punctures.

A member of the plesiomorphic *Notiobia* sub-branch then crossed (Fig. 248) the water gap between Australia-Antarctica and South America-Africa. It probably radiated and gave rise to a now largely extinct complex of groups which dispersed across South America-Africa and reached temperate Eurasia. The past occurrence of such a complex of groups is suggested by the presence of the genus *Scybalicus* in England, Europe, northern Africa, and Asia Minor. This genus belongs to the Notiobioid main branch but is the only one having the apomorphic character state of body densely pubescent. It is not closely related to other taxa of the Notiobioid main branch, which suggests past extinctions of its sister group and other relatives. In Fig. 240 the genus is shown to evolve after the South American groups of the Notiobioid main branch. This is because the South American groups presumably arose in temperate southern South America from an ancestor similar to that of the *Notiobia* sub-branch in temperate portions of Australia-Antarctica. *Scybalicus* presumably was derived from a stock which crossed the tropics of at least Africa, died out in these tropics, and became restricted to the areas now occupied by the genus. However, firm evidence as to time of origin of *Scybalicus* is lacking, and the genus may have arisen before or concurrently with the South American groups.

A member of the postulated complex of Notiobioid groups became established in temperate southern South America and ultimately diverged into the *Criniventer* and *Notiobia* stocks. The former stock possessed the apomorphic features indicated in Fig. 240 and ultimately diverged into the monotypic genera *Criniventer* and *Pseudanisotarsus*. The *Notiobia* stock retained those features found in the Australia-Antarctica ancestor but acquired the

apomorphic feature of female valvifer weakly sclerotized and with membranous or semi-membranous distal lateral margin. The *Notiobia* stock then split into the relatively plesiomorphic *Notiobia* lineage and into the more apomorphic *Anisostichus* lineage characterized by apomorphic features of mentum and submentum fused, and third elytral interval with row of dorsal setigerous punctures.

The presence or absence of a complete transverse suture dividing the mentum and submentum is elsewhere in this discussion treated as a fundamental character separating Anisodactylina into 2 main branches of evolution. However, the distribution of characters within species of *Anisostichus* and within the 3 sub-genera of the *Notiobia* lineage suggest that *Anisostichus* arose from *Notiobia* stock and that the fusion of mentum and submentum is an example of parallelism.

The extant members of the *Notiobia* stock (including *Anisostichus*) all possess a prominent mental tooth (except for a few apomorphic species of *Anisotarsus* that have secondarily lost this tooth) and have a weakly sclerotized valvifer in which the distal lateral margin is membranous. A mental tooth is a plesiomorphic character state while the type of valvifer described above is an apomorphic character state. The extant New World species of the subgenera *Notiobia* and *Anisotarsus* have, except for a few species of *Notiobia*, the dorsal membranous area of the median lobe elongate and reaching the basal bulb. The length of this membranous area is varied within the sub-genus *Diatypus* and Australian species of *Anisotarsus*. The character state of an elongate dorsal membranous area on the median lobe is thus widespread among the extant species of the genus *Notiobia* and therefore probably ancestral.

As regards *Anisostichus*, in the species *posticus* and *octopunctatus* the mentum and submentum are fused but the suture formerly separating them is still indicated by a moderately deep transverse groove; and the dorsal membranous area of the median lobe is elongate and reaches the basal bulb. In the remaining 2 species, *amoenus* and *laevis*, the former suture between the mentum and submentum is represented at most by a shallow and difficult to discern transverse impression; and the dorsal membranous area of the median lobe is short and does not even approach the basal bulb. The species *octopunctatus* and *posticus* have a type of mentum and submentum intermediate between the apomorphic form described for *amoenus* and *laevis* and the plesiomorphic form found in all *Notiobia*. And the elongate dorsal membranous area of the median lobe represents the plesiomorphic character state possessed by the assumed common ancestor of the *Anisostichus* and *Notiobia* lineages. In addition, both these lineages possess the apomorphic feature of a weakly sclerotized valvifer with membranous distal lateral margin.

The distribution of the 4 species of *Anisostichus* provides clues as to the geographical origin of this group. The species *octopunctatus* and *posticus*, here regarded as relatively primitive forms in the genus, are found in southcentral and southeastern South America (*octopunctatus* apparently being restricted to the southeastern portion). The more derived forms, *amoenus* and *laevis*, are common in the Chilean region, although *laevis* occurs elsewhere in South America. The genus *Notiobia* is apparently absent from the Chilean region. These facts suggest that *Anisostichus* evolved in the southeastern (or less likely the south-central) part of South America where the primitive species *octopunctatus* and *posticus* still survive. It then spread into the Chilean region where the more derived species *amoenus* and *laevis* arose.

Evolution of the *Anisostichus* lineage took place during the Cretaceous when South America and Africa were joined along their present northern coastlines. Evolution of the lineage could not have taken place after late Cretaceous. The two continents were by then completely separate, and the *Diatypus* group which evolved after the *Anisostichus* lineage

could not have reached Africa unless this continent was still attached to South America or at most separated by only a narrow band of ocean.

I think the sequence of evolution outlined above for the *Anisostichus* lineage is the most probable one, but I cannot conclusively prove that *Anisostichus* does not belong to the Anisodactyloid main branch. However, I can state that if *Anisostichus* were so placed, it would have no sister group since it has no close relationships to supra-specific taxa in that main branch.

The *Notiobia* lineage in temperate southern South America soon split into tropical adapted and temperate adapted sublineages. The tropical adapted sublineage possessed the apomorphic character states of: adaptations for tropical habitats; gena narrow; eye large and bulging; and clypeo-ocular prolongation present, at least in some species. Maps provided by Dietz and Holden (1970) show that the northern parts of South America and Africa were located near the present day equator during the late Jurassic and early Cretaceous (Fig. 249). Therefore, the northern parts of these two continents probably then had a tropical climate. The tropical adapted sublineage spread throughout the tropical portions of northern South America and crossed into the tropical portions of northern Africa via the northern connection of the two continents (Fig. 249).

The temperate adapted sublineage retained the plesiomorphic character states of: adaptations for temperate habitats; gena wide; eye size normal; and clypeo-ocular prolongation absent. This sublineage was not able to move into the northern tropical portion of South America which was still attached to or very close to Africa in the Cretaceous, and consequently it did not reach Africa.

The tropical adapted sublineage split with the rupture of Africa and South America. The stock thus isolated in Africa gave rise to the subgenus *Diatypus* while the stock isolated in South America gave rise to the subgenus *Notiobia*. A continental connection remained between Africa and South America until at least middle Cretaceous (Smith and Hallam, 1970), and, presumably, for some time after the rupture of this connection, interchange remained possible across the narrow band of sea separating Africa and South America. Thus, the separation of stocks in Africa and South America probably dates from early Tertiary.

The origins of *Notiobia* and *Diatypus* postulated above may be objectionable to workers who believe subgenera must always be very recently evolved entities. Only scanty fossil data is available for Carabidae. But I expect that as fossil data are gathered, it will become apparent that many specific and supra-specific taxa of Carabidae are quite old. For example, Erwin (1971) reported that a fossil Upper Oligocene or Lower Miocene tachyne carabid belongs to an extant genus and represents a species (p. 234) "hardly different from extant species now living in cloud forests of eastern Mexico (Tamps.) and other Neotropical and Nearctic species I have studied." Erwin concluded (p. 236) that "The Mexican Amber specimen represents a species of *Polyderis*, an extant group of tachyne beetles world-wide in distribution. The similarity of characteristics with present species in the same area shows that externally, at least, characteristics have hardly changed in 30 million years." A more recent time than early Tertiary for separation of the ancestors of *Notiobia* and *Diatypus* is unlikely. Such a more recent time would require invoking a whole series of postulates concerning migration across northern temperate zones and subsequent extinction in these zones. In addition, an early separation of the ancestors of *Notiobia* and *Diatypus* may be indicated by the relative degree of diversification demonstrated by described species of *Diatypus*.

Species of the subgenus *Diatypus* are placed in 2 species groups based on the structure of the ligula. The first group (formerly termed subgenus *Diatypus*) consists of species retaining the plesiomorphic state of slender ligula. The second group (formerly termed subgenus *Para-*

(*diatypus*) consists of those species with an apomorphic type of ligula bearing a laterally expanded apex. A few of the species of this group have the suture separating the mentum and submentum reduced and seemingly independently evolving towards the fused condition found in the Anisodactyloid main branch. The subgenus *Notiobia* is concentrated in tropical South America, and most of its species are probably undescribed; a study of the South American forms may also demonstrate considerable diversification within this subgenus.

The temperate adapted sublineage, which never reached Africa because of the tropical climate in the northern portion of South America, gave rise to the subgenus *Anisotarsus*. This subgenus is composed of 2 species groups: the "*Anisotarsus*" group consisting of all species found in the New World; and the "*Diaphoromerus*" group consisting of all species occurring in the Australian Region. The only appreciable differences between species of these 2 groups are: members of the "*Anisotarsus*" group have the dorsal membranous area of the median lobe elongate, reaching the basal bulb, and have the hindtarsus with the first segment shorter than II + III; members of the "*Diaphoromerus*" group have the length of the dorsal membranous area of the median lobe, and the relative lengths of the first 3 segments of the hindtarsus varying from one species to the next.

The presence of such similar species groups in the New World and the Australian Region is best explained by assuming that members of the South American temperate adapted stock crossed during the Tertiary into the Australian Region by using Antarctica and possibly several intervening islands as stepping stones. (Antarctica and Australia did not become appreciably separated until probably some time in the Tertiary (Dietz and Holden, 1970; Smith and Hallam, 1970). An alternative, but less probable, explanation for the presence of such similar groups in the New World and Australian Region is that these 2 groups are simply polyphyletic assemblages of plesiomorphic forms which arose separately in the New World and Australian Region and did not differentiate as did the other forms of Anisodactylina.

The second or Anisodactyloid main branch consists of those forms in which the mentum and submentum are either fused laterally and separate medially or completely fused. This branch is absent from the Australian region, suggesting that it did not originate there, and also is absent from South America. It probably arose in Africa or somewhere on the combined Eurasia-North America landmass after Africa had become well separated from South America. The Anisodactyloid groups while often each possessing apomorphic character states do not share synapomorphies among themselves; this suggests a moderately long period of evolution with extinction of many groups taking place during such evolution. Therefore, the Anisodactyloids probably originated in late Cretaceous or early Tertiary.

The Anisodactyloids (Fig. 241) arose from a lineage of the presumably once widespread Notiobioid main branch and then displaced this more plesiomorphic group from most areas. In Fig. 240 the Anisodactyloids are shown to arise after the genus *Scybalicus*, a remnant of the once more widespread Notiobioid main branch. A dotted line is used to emphasize that the exact time of origin of the Anisodactyloids is not clear and that *Scybalicus* is not their sister group.

Chorologies of extant groups of the Anisodactyloids suggest, but do not prove, an origin in temperate southern Africa.

Tropical Africa contains the genus *Progonochaetus* most of whose species have the mentum and submentum fused laterally but still separated medially. This genus thus contains species in which the state of the mentum and submentum is intermediate between the plesiomorphic state of completely separate and the apomorphic state of being completely fused. Therefore, it seems probable that the Anisodactyloid main branch passed through tropical Africa in an early stage of its evolution.

The Anisodactyloid main branch is today absent from the African tropics except for: *Progonochaetus*; the primarily Oriental genus *Pseudognathaphanus* which has 2 species on Madagascar; and the monotypic genus *Phanagnathus* found in the Zaire Republic (former Belgian Congo). The latter 2 genera contain species with mentum and submentum completely fused. The Madagascar species of *Pseudognathaphanus* are little differentiated from those of the Orient and probably dispersed from the Orient to Madagascar during the Pleistocene when for long periods much of the Sahara received plentiful rain (Moreau, 1966). Alternatively, the genus *Pseudognathaphanus* may have originated in tropical Africa, dispersed from there to the Orient and to Madagascar, and then became extinct in Africa. The genus *Phanagnathus* neither seems closely related by synapomorphy to other taxa of the Anisodactyloid main branch nor does it seem itself to possess many apomorphic characters. Therefore, this genus most likely arose early in the evolution of the Anisodactyloids and then became both geographically and phylogenetically isolated with extinction of its closest relatives.

Except for *Rhysopus*, the species of the Anisodactyloid genera of tropical Africa, Madagascar, and tropical Asia all possess a plesiomorphic type of ligula which is slender and not or at most only moderately expanded laterally at the apex. With the exception of *Xestonotus* and the subgenus *Amphasia*, the Anisodactyloid groups of temperate Eurasia and temperate North America have the apomorphic form of ligula with apex moderately to strongly expanded laterally. Thus, the African and Oriental groups of Anisodactyloids are relatively more plesiomorphic than the temperate North American and Eurasian ones.

In late Cretaceous, Africa was situated further south than at present (Dietz and Holden, 1970). It is thus likely that northern Africa was tropical while a large portion of southern Africa was temperate. The most probable pattern of evolution of the Anisodactyloids was one of evolution in temperate southern Africa with an early dispersal northwards through the tropics to the Orient and temperate Eurasia. The evolving Anisodactyloids presumably displaced the previous Notiobioid fauna from Africa and Eurasia (except for the genus *Scybalicus*) and displaced the Notiobioid fauna of North America (except for the genus *Notiobia*).

The ancestral Anisodactyloids then arose in temperate southern Africa and early in their evolution acquired the feature of mentum and submentum fused laterally but free medially. The ancestral Anisodactyloids twice (Figs. 250, 251) invaded more northern tropical portions of Africa, to give rise to 2 different branches. Ultimately, the ancestral stock in temperate southern Africa became extinct, quite possibly due to a contraction of southern temperate areas as Africa moved northward.

The first of the tropical adapted branches (Fig. 250) retained a partially fused mentum and submentum but acquired the apomorphic features shown in Fig. 241. This branch eventually gave rise to the subgenera *Progonochaetus* and *Eudichirus* of the mainly African genus *Progonochaetus*. One species of the subgenus *Progonochaetus*, *laevistriatus*, is present in tropical India and Burma. It may have dispersed to the Oriental Region relatively recently, such as during climatic changes of the Pleistocene; or *Progonochaetus* may once have been widespread in the Oriental Region and only recently receded from this area. The Oriental Region has not been well collected for Carabidae, and additional species of *Progonochaetus* may be present there.

The second movement of ancestral Anisodactyloid stock into tropical Africa produced the second branch with the more apomorphic feature of mentum and submentum completely fused. Some members of the second branch moved (Fig. 251) through the tropics of Africa into the tropics of the Oriental Region and radiated there. Others migrated (Fig. 251) into temperate portions of North America-Eurasia and underwent considerable radia-

tion there. Thus, the second branch was split into tropical adapted forms inhabiting the tropics of Africa and the Orient, and into temperate adapted forms inhabiting temperate regions of Eurasia. The tropical adapted forms (except for *Rhysopus*) retained the plesiomorphic slender form of ligula while the temperate adapted ones (except for *Xestonotus*) evolved an apomorphic form of ligula with a broader apex; the slender ligula of *Amphasia* is secondarily derived from the apomorphic ligula.

As it moved through Africa and into the tropics of the Orient, the second tropical adapted branch possibly gave rise to the genus *Pseudognathaphanus*. This genus today is represented in the Ethiopian Region only by 2 endemic Madagascar species which are little different from Oriental species. Thus, *Pseudognathaphanus* may have evolved in the Oriental Region and later during Pleistocene climatic changes dispersed from there to Madagascar via Africa.

The relatively apomorphic Oriental sister stock of *Pseudognathaphanus* split into the *Chydaeus* and *Rhysopus* lineages in the Oriental Region. The former lineage gave rise to the moderately apomorphic genus *Chydaeus*. The *Rhysopus* lineage possessed numerous apomorphic character states (Fig. 241) and subsequently divided to produce the genera *Harpalomimetes* and *Rhysopus*.

In the phylogeny and dispersal of North Temperate Anisodactyloids, I postulate that ancestors of all North American taxa except *Dicheirus* crossed (Fig. 252) from Eurasia into North America via the broad connection existing between western Europe and North America until some time in late Cretaceous (Dietz and Holden, 1971). Dispersal of Eurasian animals into North America is traditionally explained by invoking the Tertiary Bering Land Bridge. However, most North American Anisodactyloid groups are concentrated in the east and form a subtraction pattern towards the west. And the Anisodactyloid fauna of Eurasia is concentrated in Europe and the Mediterranean area and forms a similar subtraction pattern towards Siberia. Thus, the distribution patterns of North Temperate Anisodactyloids in most instances support dispersal into North America via the connection with Europe.

Objection may be made that if Anisodactyloids reached North America in late Cretaceous, they should have reached the present Mexican highlands before the Pliocene development of an arid zone barrier in southern Texas and northeastern Mexico (Martin and Harrell, 1957). However, there is no reason why immigrants reaching North America must immediately (if ever) have dispersed southward. They must first adapt to the new habitats presented in North America. Further, the subgenus *Anadaptus*, which I postulate arose soon after arrival of its ancestral stock in North America, does contain a species in the Mexican highlands.

The possibility that all North American Anisodactyloids arrived via the Bering Land Bridge can not be disproved. It may be that increasing aridity and cold developing in late Tertiary in Siberia and western North America destroyed the faunas of these areas. However, for all groups except *Dicheirus* I prefer the postulated crossing from western Europe to North America since distribution patterns do support this dispersal route but do not support dispersal across the Bering Land Bridge.

The temperate adapted substock in Eurasia probably early evolved the apomorphic feature of ligula apex expanded laterally. The genus *Xestonotus* is characterized by the apomorphic feature of a strongly asymmetrical median lobe but also has a ligula apex which is not expanded laterally. This genus may have evolved before the temperate adapted substock acquired the apomorphic feature of ligula apex expanded laterally, or if afterward, its narrow ligula represents a secondary reversion. Although such reversion has occurred in the subgenus *Amphasia*, it seems best to provisionally treat *Xestonotus* as having evolved just before the temperate adapted substock acquired a laterally expanded ligula apex. Since *Xestonotus* is restricted to eastern North America, its ancestor probably evolved in Eurasia,

crossed over into eastern North America via the Europe-eastern North America connection (Fig. 252), and then became extinct in Eurasia.

The temperate adapted stock in Eurasia early split into a substock retaining the plesiomorphic condition of body generally glabrous and into a substock with body generally pubescent. The possibility of the latter substock being diphyletic due to convergence is treated later in this discussion. Part of the generally glabrous bodied substock then crossed over into North America via the Europe-eastern North America connection (Fig. 252) and radiated there. The substock remaining in Eurasia in turn underwent radiation in that region.

The portion of the substock in Eurasia first divided into the *Gynandrotarsus* and *Anisodactylus* lineages. The *Gynandrotarsus* lineage was distributed across western Eurasia and eastern North America before the final rupture of the two continents in the Cretaceous. The separation of the continents divided the lineage into the *Gynandrotarsus* and *Pseudodichirus* sublineages restricted respectively to North America and Eurasia. The remaining portion of the generally glabrous bodied substock split into the *Anisodactylus* and the *Hexatrichus* branches. The first branch retained unmodified male foretibia and gave rise to the subgenera *Anisodactylus* and *Pseudanisodactylus*. The ancestor of the *Hexatrichus* branch possessed the apomorphic feature of male foretibia moderately emarginate along inner proximal margin. The branch subsequently split into: the subgenus *Hexatrichus* with male foretibia having strongly emarginate inner proximal margin; and the subgenus *Pseudhexatrichus*, with ancestral form (that is only moderately emarginate) of male foretibia.

Early in its history, the generally glabrous bodied substock in North America produced the subgenus *Anadaptus* characterized by: the apomorphic character states of short, stout hindtarsus and median lobe bearing “button”-like apical disc; and the plesiomorphic character state of stylus with glabrous basal segment. The *Aplocentrus* sister branch to the subgenus *Anadaptus* had the apomorphic character state of setae present on basal segment of stylus and the plesiomorphic character state of hindtarsus not short and stout. The *Aplocentrus* branch divided into the subgenus *Spongopus* whose sole species lacks any dorsal metallic tinge, and the subgenera *Aplocentrus* and *Pseudaplocentrus* whose ancestor had a slight metallic tinge on the dorsum.

The genus *Geopinus* most probably arose from some now extinct lineage around the time that *Anadaptus* and the *Aplocentrus* branch were produced. This genus contains only the species *incrassatus* which is highly adapted to a fossorial mode of life. This species has very short, stout hindtarsus and in general habitus resembles *Anadaptus discoideus*. However, *incrassatus* has setae on the basal segment of the stylus and does not have an apical disc on the median lobe. In addition, it has highly modified fossorial fore- and midtibia and an antennal sulcus. The most probable ancestry of *Geopinus* is indicated with a dotted line in Fig. 241.

The Eurasian substock with a generally pubescent body is composed of 2 distinct lineages united only by the apomorphic character state of body generally pubescent. The length, thickness, and density of body pubescence is considerably varied among the species of each lineage. And occasional species of *Anisodactylus*, such as *consobrinus*, have independently evolved considerable body pubescence. There is thus a possibility that the substock with a generally pubescent body is diphyletic due to convergence. However, no extant taxa in either lineage of this substock have close affinities to taxa in the generally glabrous bodied substock, and I therefore assume that the pubescent bodied substock is monophyletic.

The pubescent bodied substock early split into the genus *Amphasia* and the *Dicheirus* lineage. The ancestor of *Amphasia* was characterized by the apomorphic character state of stylus moderately dorso-ventrally flattened, apical segment with small teeth along lateral margin and small spines arising between these teeth. Since the 2 extant species of this genus

are restricted to eastern North America, the ancestor of the genus probably crossed into North America before eastern connections with Eurasia were severed in late Cretaceous. The genus ultimately split into the subgenera *Pseudamphasia* and *Amphasia*. The former subgenus has a moderately modified stylus such as in the ancestor of the lineage while the subgenus *Amphasia* has a more apomorphic type of stylus. In addition, the ligula apex of *Amphasia* has secondarily reverted to the condition of not expanded laterally.

The *Dicheirus* lineage probably evolved in Eurasia and at one time extended as far east as the present Bering Strait area. The ancestral stock of this lineage had the apomorphic character states of: frontal fovea obscured by punctures; mental tooth present; and small setae present on distal margin of basal segment of stylus. The genus *Dicheirus* is restricted to western North America, its ancestor having crossed over the Bering Land Bridge in early or middle Tertiary. The ancestor of *Dicheirus* was characterized by the apomorphic conditions of: foretibial apical spur trifid; and pronotal apical bead absent. The sister sublineage to *Dicheirus* retained the plesiomorphic condition of pronotal apical bead present at least laterally, possibly also the plesiomorphic condition of foretibial apical spur lanceolate, and acquired the apomorphic condition of dorsum brightly tri-colored. This sister sublineage subsequently split into the genera *Gynandromorphus* and *Diachromus*. The former is characterized by the apomorphic feature of a trifid foretibial apical spur while the latter has the apomorphic conditions of 2 pronotal lateral setae and the intermediate character state of foretibial apical spur swollen laterally.

Evolutionary Trends and Convergences within Anisodactylina.

The most notable evolutionary feature of the postulated phylogeny is the trend from mentum and submentum separated by a complete transverse suture to mentum and submentum completely fused. Twelve supra-specific taxa have the mentum and submentum separated by a complete transverse suture, 2 have the mentum and submentum usually fused laterally but separated medially by a transverse suture, and 23 have the mentum and submentum completely fused. There are 2 instances within the Notiobioid main branch of convergence towards the condition of mentum and submentum fused: mentum and submentum completely fused in all species of *Anisostichus*; suture between mentum and submentum narrow and apparently in process of being lost in few species of "Paradiatypus" group of subgenus *Diatypus*. A study of the possible functional advantage of a fused mentum and submentum would be worthwhile. Possibly such fusion strengthens the mouth area and enables beetles to feed on hardened material such as seeds.

Presence or absence of a mental tooth may be somewhat correlated with the state of the mentum and submentum. Most Notiobioids have a moderate sized mental tooth, clearly plesiomorphic within this main branch. Apparently the ancestor of the Anisodactyloids lacked a mental tooth for most Anisodactyloids do not have one or have only a slight swelling on the middle margin of the mentum. The mental tooth within the Anisodactyloid main branch is therefore apomorphic if present.

Several groups have evolved adaptations for burrowing. The most striking such adaptations are found in the highly fossorial *Geopinus incrassatus*. This species possesses the following features presumed to be adaptations for burrowing: a broad antennal sulcus in front of each eye for receiving antenna in repose (to protect antenna during burrowing); an apically enlarged foretibia (to strengthen foretibia and make it more effective in dirt removal); a foretibia bearing large excavate dilation externally at apex (to scoop away soil and protect tarsus); spatulate hindtibial apical spurs (useful in burrowing); a short hindtarsus (to decrease damage during digging); a narrow pronotum (to enable beetle to insert fore part of body into narrow openings prior to enlarging them); and a mandible with

deeply striate apex (resulting roughness of apex possibly of advantage in moving dirt during burrowing).

Other less fossorial Anisodactylines possess features which may also be adaptations for burrowing. Species of the genus *Dicheirus* occur on the soil surface under debris on the ground and also in worm holes and shallow burrows just beneath such debris. The body of *Dicheirus* is relatively slender, which should help in moving through burrows, and the trifid foretibial apical spur probably is advantageous in burrowing. In addition, females of *obtusus* have spatulate hindtibial apical spurs which presumably also are advantageous in burrowing.

Species of the subgenus *Anadaptus* also may be somewhat fossorial; I have taken several specimens referable probably either to *porosus* or *alternans* from shallow burrows beneath litter on the ground. Except for the somewhat stouter *discoideus*, species of *Anadaptus* are semicylindrical, which suggests adaptation for movement in burrows; all species have short hindtarsi as in *Geopinus incrassatus*; and the foretibial apical spur is thickened and subtrifid in some specimens.

Species of the subgenus *Gynandrotarsus* are semifossorial. I have taken specimens of *rusticus*, *ovularis*, *harpaloides*, *dulcicollis*, and *anthracinus* in shallow tunnels beneath debris on the ground and have taken *ovularis* and *rusticus* by digging up clumps of grass. However, the only noticeable morphological adaptation in species of *Gynandrotarsus* for burrowing is the strongly trifid foretibial apical spur.

The styli of *Pseudamphasia* and *Amphasia* form an interesting morphocline. The plesiomorphic type of stylus (Fig. 237) within the subtribe is not dorso-ventrally flattened, not laterally expanded, lacks serrations, and has 2 closely situated setae on the distal mesal margin of the apical segment. The stylus of *Pseudamphasia* (Fig. 233) is moderately dorso-ventrally flattened, moderately expanded laterally, and has an apical segment with a finely serrate lateral margin bearing very small spines between the serrations. The stylus of *Amphasia* (Fig. 234) is even more apomorphic and is strongly dorso-ventrally flattened, strongly expanded laterally, and has an apical segment with a prominently serrate lateral margin bearing stout spines between the serrations.

The valvifers within 5 subgenera of *Anisodactylus* form a morphocline from a triangular ancestral type (Figs. 217, 218, 219) with distal setae, to a subtriangular type which lacks distal setae, and bears a distal concave area (Fig. 130). The ancestral type is found in *Anisodactylus* and *Pseudhexatrichus*. An intermediate subtriangular type with distal setae (Fig. 222) is found in *Hexatrichus*. In *Pseudodichirus* (Fig. 220) the valvifer in addition to being subtriangular is further modified by loss of all distal setae. Lastly, in *Gynandrotarsus* the valvifer not only is subtriangular and lacks distal setae but has acquired a distal concave area (Fig. 130).

Table 3 (p. 435) summarizes instances of convergence noted among supra-specific taxa of Anisodactylina. Two of these instances are further discussed here. In the past, several polyphyletic supra-specific groups have been defined on the basis of their species possessing a trifid foretibial apical spur. Examination of other characters has convinced me that the trifid type of spur has arisen by convergence within 4 monophyletic supra-specific groups: (1) in 3 species of the subgenus *Anisodactylus*; (2) in the single species of the genus *Rhysopus*; (3) in all species of the subgenus *Hexatrichus*; and (4) in the common ancestor of the sister subgenera *Pseudodichirus* and *Gynandrotarsus*. The species of the genera *Gynandromorphus* and *Dicheirus* also possess a trifid foretibial apical spur, due to convergence or not. If not, then the spur of the sole species of *Diachromus* (sister genus to *Gynandromorphus*) has secondarily reverted to the non trifid state. Trifid foretibial apical spurs may also be evolving in other groups such as *Anadaptus*, *Gnathaphanus*, and *Scybalicus* in which few or all members of some species have the spur slightly angulate on each side or even some-

what subtrifid. The evolutionary reason for convergence in trifid spurs is probably increased efficiency in burrowing.

The shape of the ligula also demonstrates interesting convergences. The plesiomorphic type of ligula is slender and with apex not or only very slightly laterally expanded. An apomorphic type of ligula in which the apex is moderately to strongly expanded laterally has independently arisen in: (1) some specimens of *Notiobia (Anisotarsus) tucumana*; (2) the "Paradiatypus" species group of the subgenus *Diatypus*; (3) the genus *Criniventer*; (4) the genus *Rhysopus*; and in all temperate adapted Anisodactyloids except for the genus *Xestonotus*. In addition, the ligula of *Amphasia* has secondarily reverted back to the narrow form without an expanded apex.

Phylogeny of the New World Species of the Subgenus *Anisotarsus*.

Table 4 (p. 436) summarizes the plesiomorphic and apomorphic character states employed in reconstructing the phylogeny illustrated in Fig. 242. The ancestor of *Anisotarsus*, which arose in temperate areas of southern South America, possessed the plesiomorphic character states listed in Table 4 (p. 436) and in addition had: body and appendages rufopiceous to black, dorsum lacking metallic color or tinges; microsculpture of isodiametric mesh; and dorsal membranous area of median lobe extended to basal bulb.

In the early or middle Tertiary a species of *Anisotarsus* dispersed to North America by crossing water gaps between various islands in the present Central American and Caribbean areas. This species early gave rise to the *cyanippa* and *terminata* branches. The first branch retained the ancestral feature of wide gena while the second one acquired apomorphic narrow gena. The *cyanippa* branch subsequently split into the *cyanippa* and *brevicollis* lineages. The former lineage retained the plesiomorphic feature of only 2 ambulatory setae on the sixth abdominal sternum of males but possessed the apomorphic features of pronotal posterior angle moderately to strongly rounded and hind wing vestigial or dimorphic. The lineage ultimately produced the Mexican species *hilariola* and *cyanippa*. I have seen 1 male of *hilariola* with 4 ambulatory setae on the sixth abdominal sternum; this may be an aberrant specimen, or the number of such setae may vary in males of *hilariola*, or a relationship with the *brevicollis* lineage may be indicated. The *brevicollis* lineage retained the ancestral type of pronotal posterior angle and hind wing but possessed the apomorphic feature of 4 ambulatory setae on the sixth abdominal sternum of males. The primarily Mexican species *brevicollis* is the only extant representative of this lineage.

A major weakness in linking the *brevicollis* and *cyanippa* lineages is the apparent lack of synapomorphies between them. However, the *brevicollis* lineage certainly does not seem to belong to the *terminata* branch, and chorology suggests that its closest extant relative is the *cyanippa* lineage. Extinctions in both the *brevicollis* and *cyanippa* lineages as well as of any possible intermediate lineages may explain the lack of synapomorphies.

Due apparently to a complex history of radiation and to subsequent extinctions of many species, only the *nitidipennis* lineage within the *terminata* branch can be defined by clearly apomorphic features. The *nitidipennis* lineage is composed of the species *nitidipennis* and *schlingeri* characterized by the apomorphic states of eye usually relatively small and pronotal side straight or sinuate basally. The 2 species are geographically disjunct and appear to be sister species.

The 3 species *flebilis*, *purpurascens*, and *terminata* are not united by any clearly apomorphic characters but probably form a single lineage, the *terminata* lineage, for the following reasons. The species *flebilis* and *purpurascens* were formerly considered to be subspecies of a single common species, because of their strikingly similar general habitus and because their pronotal sides were moderately convergent basally. Indeed, their general habitus is so

similar that it is often difficult to separate teneral females of *purpurascens* from females of *flebilis*. The legs and first antennal segment of these 2 species are always testaceous to rufous in color. Such coloration occurs in several other species of *Anisotarsus*, but the more common and possibly, therefore, more plesiomorphic condition is that of darker legs and antenna. The species *flebilis* is known only from Guadalupe Island, southern Baja California, and the Mazatlan region of Mexico, and it may represent an isolated relict species of a formerly widespread ancestral stock.

The species *purpurascens* shares relationships to *terminata*, but these relationships are complicated by the wide character variability found in *terminata*. The species *purpurascens* has a general habitus very similar to that of some specimens of *terminata* which have the pronotal sides moderately convergent basally, pronotal lateral depression obsolete, and elytron lacking a greenish tinge. These character states occur in occasional specimens of the Texas, Florida, and Mexico morphs of *terminata*, and some specimens of the 2 species appear so similar in external features that they are very difficult to separate. The median lobe of *purpurascens* is stout in form and very similar to that found in the northern morph of *terminata*. The median lobes of Texas, Florida, and Mexico morphs of *terminata*, however, are typically more slender in form than that of the northern morph or of *purpurascens*. And specimens of the northern morph differ from *purpurascens* in having a wide prominent pronotal lateral depression. Also, *terminata* always has the same light colored legs and first antennal segment as do *purpurascens* and *flebilis*. It is reasonable to conclude that these 3 species came from the same ancestral stock.

The species *virescens*, *maculicornis* and *picea* are evidently derived from the same ancestral stock which gave rise to the *terminata* and *nitidipennis* lineages. However, it would appear that these 3 species are the survivors of an early species radiation or radiations as they do not show close relationships to each other or to either the *nitidipennis* or *terminata* lineages. The species *picea* is somewhat isolated from *virescens*, *maculicornis* and the *terminata* lineage by the combination of 4 setae on the sixth abdominal sternum in males and pronotal microsculpture obsolete medially. Since both *picea* and *schlingeri* have 4 setae in the male, *picea* may possibly be the sole survivor of a once larger lineage containing species linking the *terminata* and *nitidipennis* lineages. The species *virescens* and *maculicornis* do not show close relationships to *picea* or to the *terminata* or *nitidipennis* lineages. In the absence of further data, it is impossible to state more than they probably were derived from the same general stock as these forms due to their also sharing the plesiomorphic condition of wide gena.

The *Anisotarsus* stock which remained in South America early acquired the apomorphic features of distal setae present on elytral intervals III, V, and VII and internal sac of the median lobe lacking a large spine. It then split into the *tucumana* and *mexicana* branches.

The *tucumana* branch was characterized by the apomorphic features of pronotal posterior angle moderately to strongly rounded and sixth abdominal sternum of males with 4 ambulatory setae. It soon divided into 2 lineages: the *cupripennis* lineage whose members possessed the plesiomorphic condition of a prominent mental tooth; and the *tucumana* lineage whose members possessed the apomorphic condition of mental tooth absent or vestigial. The *cupripennis* lineage is composed of 8 named forms and needs further study before the exact relationships of its forms can be elucidated.

The *tucumana* lineage contains 2 named South American species, *tucumana* and *bradytoides*, and 1 unnamed species which in this discussion and in Fig. 242 is termed species "A". Additional study of South American *Anisotarsus* may reveal more undescribed species and change some of my conclusions presented below concerning the evolutionary history of this lineage.

The *tucumana* lineage evidently gave rise early in its history to a species or group of species possessing only a vestigial mental tooth. This ancestral species or species group in turn produced the species *bradyoides* possessing a vestigial mental tooth and the plesiomorphic conditions for the ligula, abdominal pubescence, and median lobe. Also this ancestral species or species group gave rise to a species completely lacking a mental tooth and possibly possessing some additional setae on abdominal sterna IV and V. This species then ultimately gave rise to *tucumana* and to species A. The latter species in addition to lacking a mental tooth possesses the apomorphic condition of having a few fine short additional setae on the fourth abdominal sternum. The species *tucumana* possesses the additional apomorphic features of: ligula with apex moderately to prominently widened as in *Anisodactylus*; abdominal sternum IV and V bearing extra setae (more numerous in male); posterior margin of hind femur with 10 to 12 setae; and median lobe highly asymmetrical. Also the internal sac of the median lobe of *tucumana* apparently regained a large prominent spine, unless some past ancestors of the *tucumana* lineage retained this feature, or unless the *tucumana* lineage is polyphyletic. The possession of these strikingly apomorphic character states suggests that *tucumana* may be the end result of a serial evolution of several species from the original ancestor of species A.

The *mexicana* branch possessed the apomorphic feature of pronotal lateral bead very prominent, and the additional feature of females having eighth abdominal tergum with obtusely angulate apex. During early Pliocene a member migrated to North America via the newly established Central American connection between North and South America. The member migrating to North America gave rise there to the *mexicana* lineage while the stock remaining in South America produced the *chalcites* lineage.

The *chalcites* lineage acquired the apomorphic features of metallic tinges on dorsum and 4 ambulatory setae on sixth abdominal sternum of males, and retained the postulated ancestral type of female eighth abdominal tergum. It subsequently split to produce the named forms *chalcites* and *amethystina*.

The ancestor of the *mexicana* lineage retained the ancestral features of non-metallic tinged dorsum and male sixth abdominal sternum with only 2 ambulatory setae. The lineage produced the species *lamprota*, which evolved metallic tinges but retained the ancestral type of female eighth abdominal tergum, and the species *mexicana* which retained a non-metallic dorsum but acquired the apomorphic features of female eighth abdominal tergum rounded at apex and antennal segments short.

The apomorphic character state of 4 ambulatory setae on male sixth abdominal sternum has arisen 5 times by convergence, and the apomorphic character state of rounded pronotal posterior angle did so twice. These convergences are not surprising since the characters these states represent are not especially constant within Anisodactylina. The instances of convergence in number of male ambulatory setae could be reduced to 4 by connecting the *brevicollis* lineage to the *tucumana* branch. However, this would require: an additional invasion of North America; secondary loss in the *brevicollis* lineage of distal setae on elytral intervals III, V, and VII; and secondary regaining in the *brevicollis* lineage of a large spine on the internal sac of the median lobe. Similarly, and over similar objections, convergence in rounded pronotal posterior angles could be eliminated by connecting the *cyanippa* lineage to the *tucumana* branch.

Except for the *mexicana* lineage, the North American and South American species do not show any close phylogenetic relationships. The reasons for this general lack of close phylogenetic relationships are discussed in the section on historical zoogeography.

Remarks on the Phylogeny of the Species of the Subgenus *Notiobia*.

In this paper I am revising only 10 of the 24 named species of this subgenus. Several of these revised species are recorded from Central or South America, and additional collecting will undoubtedly result in additional ones being recorded from these regions. In several instances I have noted that the closest relatives of Mexican species appear to be found in Central or South America, and I have seen many specimens from Central and South America which appear to be new species. I feel that it would be unproductive to attempt constructing a phylogeny of *Notiobia* (*s. str.*) until the Central and South American forms are better known.

Phylogeny of the Species of the Subgenus *Gynandrotarsus*.

Table 5 (p. 438) summarizes the plesiomorphic and apomorphic character states employed in the reconstructed phylogeny presented in Fig. 243. The ancestor of *Gynandrotarsus* possessed the plesiomorphic character states listed in Table 5 (p. 438) and in addition had: body with microsculpture of isodiametric mesh; 4 ambulatory setae on male abdominal sternum VI; and no large armature on internal sac of median lobe.

The ancestor of *Gynandrotarsus* most likely arrived in eastern North America during late Cretaceous or early Paleocene via the connection with the European part of Eurasia. The ancestor then produced the *harpalooides* and *merula* stocks. It seems most likely that the common ancestor of these stocks possessed the character state of a raised transverse ridge behind the clypeal apex. Such a transverse ridge is present in all species of the *merula* stock and in the species *opaculus* of the *harpalooides* group. It is more probable that this structure was lost in the other species of the *harpalooides* stock than that it evolved independently in *opaculus*. It should be mentioned here that *opaculus* is not intermediate between the *harpalooides* and *merula* stocks simply because females of *opaculus* have the first segment of the foretarsus strongly laterally expanded and most specimens of both sexes have a slight dorsal greenish tinge. In my opinion, the presence of a raised transverse ridge behind the clypeal apex is a plesiomorphic character state within the subgenus *Gynandrotarsus* while it is an apomorphic character state when comparing the subgenera of *Anisodactylus*. Conversely, the absence of such a ridge, which is plesiomorphic in the genus *Anisodactylus*, is apomorphic within *Gynandrotarsus*.

The *harpalooides* stock was characterized by the apomorphic character state of first foretarsal segment slightly to moderately expanded laterally in females, and by the plesiomorphic character states of: clypeo-ocular prolongation; raised transverse ridge behind clypeal apex; and apical disc on median lobe. This group subsequently split into the *harpalooides* and *texanus* lineages. The first lineage possessed the apomorphic character states of: median lobe lacking apical disc; greenish tinge present on dorsum; and first segment of female foretarsus strongly expanded laterally. The *texanus* lineage in turn retained the ancestral states of these characters.

The *harpalooides* lineage ultimately gave rise to the species *opaculus* and *harpalooides*. The species *opaculus* has prominent dorsal microsculpture whereas *harpalooides* and the two extant species of the *texanus* lineage have reduced dorsal microsculpture. Therefore, there may have been a series of ancestral species giving rise ultimately to *opaculus*.

The *texanus* lineage finally produced the species *texanus* and *dulcicollis*. As these two species are not related by any special synapomorphies, and as they are not extremely similar phenotypically, they may represent the sole survivors of a larger assemblage of species derived from the *texanus* lineage.

The *merula* stock was characterized by the apomorphic features of clypeo-ocular prolongation absent and pronotum moderately widened basally.

Evidently, at an early stage in its evolution the *merula* stock produced the now monotypic *haplomus* branch characterized by the apomorphic character states of: pronotal lateral bead obsolescent anteriorly, fine elsewhere; microsculpture of frons of isodiametric punctures; elytral subapical sinuation prominent; and pronotum prominently widened basally. The latter feature is also possessed by the species *merula*, but I believe this is due to convergence.

The remaining 5 species of the *merula* stock form the *merula* branch which is defined only on the basis of symplesiomorphy. Therefore, the following postulated sequence of evolution is based on chorology and relative degree of apomorphy shown by each species. The *merula* branch produced the now widespread monotypic *rusticus* lineage, characterized by the apomorphic feature of median lobe lacking apical disc. The complimentary *merula* lineage retained the plesiomorphic feature of median lobe with apical disc present and split into the *ovularis* and *merula* sublineages. The *merula* sublineage possessed the apomorphic feature of humeral tooth present while the *ovularis* sublineage retained the plesiomorphic state of tooth absent. The *merula* sublineage includes *merula* and *anthracinus*, which have identical median lobes, show spatial vicariance (Figs. 160, 161), and are recently evolved sister species. The *ovularis* sublineage gave rise to *ovularis* and *darlingtoni*, which are not united by clearly apomorphic character states but have very similar general habitus.

ZOOGEOGRAPHY

Introduction

This section discusses the zoogeography of supra-specific taxa of Anisodactylina and of species of *Anisotarsus*, *Notiobia* (*s. str.*), and *Gynandrotarsus*. Both contemporary and historical zoogeography are treated for *Anisotarsus* and *Gynandrotarsus*. Information on ecology of species of the other 35 groups is limited as is information on past climates, flora, and fauna of the areas they inhabit. It was necessary to use all available information on historical zoogeography of the supra-specific taxa in order to elucidate their phylogenetic relationships. Consequently, this information has been incorporated into the section on phylogeny of the supra-specific taxa. And the zoogeography of the species of *Notiobia* (*s. str.*) is only very briefly treated for reasons outlined in the subsection on them.

Contemporary Zoogeography of the Subtribe Anisodactylina.

The 6 major faunal regions (Nearctic, Neotropical, Palearctic, Ethiopian, Oriental, and Australian) were originally proposed by Sclater (1858), on the basis of bird distributions, confirmed by Wallace (1876) for vertebrates and some invertebrates, and reconfirmed and further discussed by Darlington (1957) for vertebrate distribution. Darlington (1957) stated that Madagascar was traditionally placed in the Ethiopian region, but that he preferred to treat it separately. Heilprin (1887) combined the northern regions, the Palearctic and Nearctic, into a Holarctic Region on the basis of vertebrates shared between the two areas. Kuschel (1963) discussed arguments for treating southern South America, southern Africa, Antarctica, and the Australian area as a distinct "Austral Region". He pointed out (p. 448) that the distribution of weevils "definitely points to an Austral Region; but I would also say that such a big step would need to be based on many groups."

I agree with Kuschel that such a "big step" should be based on many groups. I also believe that invertebrates in general, and insects in particular, have been neglected when zoologists attempt to divide the world into major faunal regions. Workers revising previously little understood groups should endeavor to analyze the regional divisions suggested by the distribution of included taxa. This analysis should be done so that future zoogeographers

can consider possible changes in the major faunal regions as suggested by distributional data from many different groups of invertebrates. I endeavor below to analyze the correlation of distribution of groups of Anisodactylina with the 6 major faunal regions as defined by Wallace (1876) and as modified by Heilprin (1887), Darlington (1957), and Kuschel (1963).

The bottom of Table 6 (p. 440) gives the distribution of groups in terms of the 6 faunal areas as defined by Wallace (1876); genera and subgenera are treated as equivalents and termed "groups".

Data from Table 6 (p. 440) indicate that the Nearctic and Palearctic Regions should be retained as separate major faunal regions. Ten or 83 percent of the 12 groups found in the Nearctic Region are endemic while 6 or 67 percent of the groups found in the Palearctic are endemic. The 2 regions share only 1 group, the subgenus *Anisodactylus*.

The Palearctic Region, consisting basically of temperate Eurasia, contains a single center of concentration embracing Europe (especially the southern part) and the lands surrounding the Mediterranean. Six of the 9 groups present in the Palearctic Region are endemic to this center of concentration: *Scybalicus*, *Pseudohexatrichus*, *Hexatrichus*, *Pseudodichirus*, *Gyndromorphus*, and *Diachromus*. An additional group, the subgenus *Anisodactylus*, has some of its species occurring in this center of concentration.

The eastern part of temperate Eurasia (Siberia, north and central China, Japan, and Korea) is relatively depauperate in number of groups. Four groups, *Chydaeus*, *Harpalomimetes*, *Anisodactylus*, and *Pseudanisodactylus* occur there. The only group which appears endemic to eastern Eurasia is *Pseudanisodactylus* which apparently is restricted to Japan, Korea, and China. *Chydaeus* on mainland Eurasia enters only the southern part of the Palearctic Region in Tibet and central China and offshore extends only to Japan. The 2 species of *Harpalomimetes* are mostly concentrated in the Oriental Region, and only one of them extends as far north as Japan and thus into the Palearctic Region. The species of *Anisodactylus* in Eurasia generally have wide distributions ranging from temperate Europe to Japan.

The Oriental Region consists essentially of tropical southern Eurasia together with the Philippines and the Indo-Australian Archipelago. Darlington (1957) pointed out the lack of sharp boundaries for this region. The western boundary in India is uncertain, and the dry country of northwestern India has an impoverished vertebrate fauna with transitions occurring from east to west and from north to south. In the northeast the Himalaya forms a natural boundary, but this boundary occurs several degrees north of the tropics. Further east the boundary of the Oriental Region becomes more difficult to fix, and there is a broad, complex transition between the Palearctic and Oriental Regions. And the Oriental fauna forms a broad complex transition with the Australian fauna beyond Java and Borneo.

The distributions of groups of Anisodactylina support these views of Darlington, and the lack of sharp natural boundaries for this region is reflected by the low rate of endemism here. Of the 9 groups represented, only *Rhysopus* is endemic. The genus *Chydaeus* centers in southern China, northern India, and Sikkim of the Oriental Region but also in Tibet which is north of the Himalayas and thus in the Palearctic Region. The genus extends to central China, and Japan, and eastward on mountain tops along the Indo-Australian Archipelago to New Guinea. *Harpalomimetes* is centered in the Oriental Region but does occur in Japan and goes as far towards Australia as the Philippines. *Hypharpax* is an Australian group which has 3 species reaching as far into the Oriental Region as Java. The genus *Gnathaphanus* is another Australian group, but species are in the Indo-Australian Archipelago, and a few widely distributed species reach India and the Philippines. *Crasodactylus* extends from western India to the Zaire Republic (former Belgian Congo), which is well inside the Ethiopian Region. The subgenus *Anisodactylus* is represented by 1, possibly 2, species in India, Burma, and Indochina but is predominately concentrated in the Palearctic

and Nearctic Regions. The Ethiopian centered subgenus *Progonochaetus* is represented by a single species in tropical India and Burma. And the genus *Pseudognathaphanus* contains 5 species in the Oriental Region but also has 2 on Madagascar.

As defined by Wallace (1876), the Australian Region consists of Australia, Tasmania, New Guinea, New Zealand, New Caledonia, the Celebes and various small islands located to the east of the Celebes and to the north and east of Australia. Some zoogeographers (such as Darlington, 1957) prefer to treat New Zealand and New Caledonia as simply adjacent islands rather than as part of the Australian Region. This is because of the supposed antiquity of these islands and because of the high rates of endemism in animal groups present on them.

New Caledonia contains no endemic groups of Anisodactylina. However, it does have 1 species of *Anisotarsus* and 2 species of *Gnathaphanus*. These 3 species have presumably recently arrived on New Caledonia by dispersal across present water gaps. *Anisotarsus* is centered primarily in the New World and in Australia and Tasmania. And *Gnathaphanus* is predominately centered in Australia and to a lesser degree in the Indo-Australian Archipelago. With the exception of the 1 species of *Anisotarsus* (presumably derived from Australia rather than the New World), New Caledonia shows no zoogeographical relationships with other major faunal regions and would seem best placed within the Australian Region.

New Zealand contains 4 groups of Anisodactylina; two of these, *Allocinopus* and *Triplosarus*, are endemic. *Allocinopus* has undergone considerable evolution in New Zealand but presumably once shared with *Hypharpax*, *Cenogmus*, and *Crasodactylus* a common ancestor which originated in Australia. *Allocinopus* shows no close relationships with other groups and appears to have been evolving on New Zealand for a considerable period of time. New Zealand also contains 2 species of the New World, Australia and Tasmania centered *Anisotarsus* and 1 species of the Australia and Tasmania centered *Hypharpax*. The presence of 2 endemic, highly evolved, and only slightly related groups on New Zealand suggests long separation. But on the basis of Anisodactyline distributions, New Zealand has a definite zoological relationship with Australia and Tasmania, and it seems best to follow Wallace (1876) and treat New Zealand as a subregion of the Australian Region.

The continent of Africa is clearly divided into Palearctic and Ethiopian Regions by the distribution of groups of Anisodactylina. Except for 1 species of *Crasodactylus*, Africa north of the Sahara Desert contains only Palearctic groups, namely *Anisodactylus*, *Diachromus*, *Pseudodichirus*, *Hexatrichus*, *Pseudohexatrichus* and *Scybalicus*. The Sahara Desert is apparently devoid of Anisodactylines except possibly for the species *Crasodactylus punctatus*, which is reported by Basilewsky (1950) to occur in sandy places from India to the mountains of Kivu in the Belgian Congo. Africa south of the Sahara Desert constitutes the Ethiopian Region minus Madagascar and associated smaller islands. The Ethiopian portion of Africa contains groups which, except probably for *punctatus* of the genus *Crasodactylus*, contain species adapted to tropical habitats. The temperate southern tip of Africa does not appear to have an Anisodactyline fauna. Of the Ethiopian groups: *Crasodactylus* is also found in the Palearctic and Oriental Regions; *Pseudognathaphanus* is centered in the Oriental Region but has 2 species on Madagascar; *Scybalicus* has 2 species in the Palearctic Region; and *Progonochaetus* has 1 species in India and Burma and 37 in the Ethiopian Region. The remaining 3 groups are endemic to the Ethiopian Region.

The presence of distinct Palearctic and Ethiopian faunas of Anisodactylines north and south respectively of the Sahara Desert suggests that this desert serves as a good boundary between the Palearctic and Ethiopian Regions. Ball (personal communication) has commented on the effectiveness of the Sahara Desert as a barrier to dispersal of carabids in general. The Sahara Desert is similarly effective in barring dispersal of birds, plants, and butter-

flies, but it is not effective in barring dispersal of mammals as much of the Palearctic part of Africa is inhabited primarily by Ethiopian forms. (Moreau, 1966).

Wallace (1876) treated Madagascar as a subregion of the Ethiopian Region. Madagascar possesses 2 groups of Anisodactylina, *Pseudognathaphanus*, with 2 species endemic to Madagascar and 5 in the Oriental Region, and *Progonochaetus*, with 3 species endemic to Madagascar, 34 on the Ethiopian portion of Africa, and 1 in the Oriental Region. Madagascar thus has equal zoogeographic relationships with the Ethiopian portion of Africa and with the Oriental Region. Geographically, the best placement of this island is probably as a subregion of the Ethiopian Region, but with regards to the Anisodactylina fauna it could almost as well be treated as a subregion of the Oriental Region.

The groups occurring in the Nearctic Region are predominately centered in temperate and warm temperate areas of the eastern portion of North America. Six groups, *Spongopus*, *Pseudaplocentrus*, *Geopinus*, *Xestonotus*, *Amphasia*, and *Pseudamphasia*, form a subtraction pattern towards the west and are confined to the eastern United States and southeastern Canada. The subgenus *Gynandrotarsus* is centered in the eastern United States but has some species in the western part and in temperate areas of Mexico. The subgenus *Anisotarsus* is centered in northern Mexico, is moderately abundant in number of species in the eastern United States and southeastern Canada, and is poorly represented in the western United States. Three groups, *Anisodactylus*, *Anadactus*, and *Aplocentrus*, are equally well represented in both eastern and western United States or in eastern and western portions of southern Canada. The genus *Dicheirus* is restricted to the western half of North America.

The Neotropical Region contains only 5 groups, 1 of which is shared with the Nearctic. The shared group, *Anisotarsus*, is centered in temperate and warm temperate areas of the Australian, Nearctic and Neotropical Regions but in the latter 2 regions has a few species which extend along the tops of mountains into areas whose lowlands are tropical. The distribution of Anisodactylina within the Neotropical Region strongly supports Wallace's (1876) division of it into tropical and temperate subregions. Three of the 4 endemic groups of the Neotropical Region, *Criniventer*, *Pseudanisotarsus*, and *Anisostichus* are apparently restricted to temperate areas in southern South America. The 4th, *Notiobia* (s. str.), is restricted to tropical areas. As discussed above, the subgenus *Anisotarsus* within the Neotropical Region is centered in temperate and warm temperate areas and extends into tropical areas only along mountain tops. The Anisodactylina fauna of the Neotropical Region thus is composed of distinctly tropical (1 group only) and temperate elements (4 groups).

The distribution of groups of Anisodactylina does not offer much support to the concept discussed by Kuschel (1963) of combining temperate southern South America, temperate southern Africa, and the Australian Region into a single Austral Region. The only close relationship among Anisodactylina in these areas is the occurrence of *Anisotarsus* in both the New World and the Australian Region. The 3 endemic genera in temperate southern South America share no close relationships with the 3 endemic groups in the Australian Region. And temperate southern Africa does not appear to contain an Anisodactylina fauna.

The supra-specific taxa of Anisodactylina were analyzed to determine whether groups are more abundant in temperate or in tropical regions. Table 7 (p. 443) divides the groups into those found in temperate and tropical habitats. In the preparation of this table, the distribution of species in each group was compared with climate and vegetation region maps in the Hammond 1967 World Atlas and Gazetteer. Groups containing both tropical and temperate adapted species were marked under both the temperate and tropical columns. Species inhabiting mountain tops in areas with tropical lowlands were classified as temperate adapted despite the tropical conditions of surrounding lowlands. I am aware that the climate of mountain tops in tropical areas is not completely equivalent to that of temperate areas, but

species living there are exposed to colder conditions and also probably to less biotic competition as are species in "true" temperate areas. A result of this method of classification is that *Chydaeus* is considered as a temperate rather than a tropical group because its species are apparently restricted to mountainous areas within the tropics. And *Anisotarsus* is treated as a completely temperate group although several of its species are found on mountains in areas with tropical lowlands.

Table 7 (p. 443) indicates that a total of 30 groups are found in temperate habitats, and that 26 of these groups are restricted to such habitats. Only 11 groups are found in tropical habitats, and 4 of these groups are also found in temperate ones. The subtribe Anisodactylina is clearly more abundant in number of groups in temperate than in tropical areas. A likely explanation for this is that Anisodactylines originated in temperate areas (as postulated in the phylogeny section) and are as yet in general less adapted to tropical habitats.

One might ask whether the greater number of supra-specific taxa in temperate areas results from the fauna of these areas being better known. This might in part be the answer. However, the fauna of tropical Africa is certainly at least moderately well known but contains only 4 endemic and 3 nonendemic groups, while the fauna of the Nearctic Region contains 10 endemic and 2 nonendemic groups. And South America contains 4 temperate adapted groups (3 of which are endemic) and only a single tropical adapted one. Temperate portions of South America are no better collected than tropical ones.

Table 6 (p. 440) presents information on the number of species in each of the 6 faunal regions and information on the average number of species per taxon in each such region. The table indicates that in terms of average number of species per group, the 6 faunal regions rank moderately well according to the postulated sequence of evolution and dispersal of Anisodactylines, that is, areas presumed to have older Anisodactyline faunas tend to have more species per supra-specific taxon. For example, the Australian Region which is the presumed origin of Anisodactylina ranks first with an average of 12.7 species per group while the Oriental Region ranks last with 3.3 species per group. The probable reason for areas with older Anisodactyline faunas having more species per group is explosive radiation of supra-specific taxa immediately after colonization followed by evolution of additional species in the already evolved groups. Thus, the number of species per group would increase according to the age of the Anisodactyline fauna.

The low values for the Palearctic and Nearctic Regions may be due not only to their Anisodactyline faunas being relatively young but to extinction of many species during glacial periods of the Pleistocene. Some supra-specific taxa no doubt also became extinct during such periods, but their percentage of extinction may have been much less than that for species. A greater percentage of species extinction during glacial periods may explain the low value for the large Palearctic Region, which presumably has a slightly older Anisodactyline fauna than the Nearctic Region, yet only approximately half as many species. A possible explanation for such greater species extinction in the Palearctic Region is the differing arrangement of mountains. The mountains of the Nearctic Region run predominately from north to south and thus probably did not greatly hinder movement of species southward into refugia during Pleistocene glacial periods. In contrast, mountains of Eurasia run predominately east to west and therefore probably prevented southward movement of many species during glacial periods.

Contemporary Zoogeography of the Subgenus *Anisotarsus*, Especially in North America.

Within the New World the subgenus *Anisotarsus* is generally amphitropical in its distribution, being centered in temperate to warm temperate areas of North and South America (Fig. 132). Thirteen species are found in North America, and only 2 of these, *terminata* and *mexi-*

cana, extend into Central America. The other 11 species extend no farther south than the edge of the Mexican plateau in the Golfo de Tehuantepec region. And except for *lamprota* which possibly occurs in tropical areas along the eastern coast of central Mexico, these 11 species are found in areas with a temperate or warm temperate climate. Specimens of *terminata* found south of the Mexican plateau are restricted to highland and mountain regions of 1,000 feet or higher which presumably are warm temperate or temperate in climate. The species *mexicana* is similarly restricted except for 2 males recorded from Merida, Yucatan, Mexico. The species in South America show a similar temperate and warm temperate distribution except for *chalcites* and *amethystina* which occur in tropical areas. All other South American forms are restricted either to temperate and warm temperate areas in the central part of the continent or to the Andes and other elevated non-tropical areas in the northern part. None of the South American species extend into Central America.

It is interesting that *lamprota*, *chalcites* and *amethystina*, which possibly occur in tropical environments, and *mexicana*, which extends into Central America along mountains and highlands, constitute the *mexicana* lineage. As discussed in the sections on phylogeny and historical zoogeography, this is the only instance in which North and South American species of *Anisotarsus* show close phylogenetic connections.

The distribution of each of the 13 North American species is shown by dots on separate maps for each species. In Fig. 253 the ranges of all the species are each delimited by a line drawn around the outermost dots for each species. This figure shows that species are most numerous in southwestern Texas, northern and Central Mexico, less numerous in the eastern half of North America, few in western United States, and absent north of the fiftieth parallel. Further, the 3 species found in California, Arizona, and New Mexico are merely northward extensions of species primarily centered in Mexico. These 3 species are restricted to mountains in Arizona and New Mexico, while the single one reaching California, *purpurascens*, is found there along the coast and in mountains or other elevated areas of the interior. The eastern part of the United States north of the Gulf region contains 4 species, 3 of which are widespread. This suggests that the area presently lacks effective barriers to dispersal of species within it. It also has certain implications concerning historical zoogeography which are discussed in that section.

It is also evident from Fig. 253 that the subgenus in North America is primarily adapted to temperate and warm temperate environments with summer rains. Species do not extend far north of the Canadian border, and the 3 that are found north of the border are all wide ranging and centered in warm temperate areas. The decrease in number of species northward is probably due to effects of Pleistocene glaciation (Howden, 1969), and also to a lack of tolerance for cold environments. Only 2 species enter the tropics of Central America, and these 2 species (except for the single *mexicana* from Merida) are restricted to mountains and highlands which presumably have subtropical or even temperate climates. The decrease in species towards the west within the United States is correlated with decreasing summer rainfall. For example, Arizona which receives summer rainfall has 3 species while California which very rarely receives summer rainfall has only 1 species.

The species *flebilis* has a disjunct distribution which possibly is also correlated with the amount of summer moisture. It occurs on Guadalupe Island, southern Baja California, and the Mazatlan region of western Mexico. Guadalupe Island has a persistent summer fog belt in the summit section (Axelrod, 1967) and has a milder and moister climate than the immediately adjacent mainland (Savage, 1967). The persistent summer fogs and milder and moister climate probably are analogous in their effects to summer rain. I suspect that all specimens recorded from Baja California actually were collected in Laguna woodland areas of the Laguna Mountains which have a cooler, moister climate than the surrounding low-

lands (Axelrod, 1958). And the Mazatlan region also receives summer rains.

The distribution of species has a limited correlation with topography. Species occurring in Mexico are primarily centered in the highlands while those found in New Mexico and Arizona are restricted to mountains or the foothills of mountains. In the warm temperate eastern United States species range over mountains and rivers which are barriers to other groups of Carabidae. The Rocky Mountains in the western United States may possibly serve as a barrier, but decreasing summer rainfall is probably a more important factor.

Central America contains only 2 known species of *Anisotarsus*. Erwin (1970) working on *Brachinus* also found a marked reduction in the number of known species from this area and concluded this is probably due to under-collecting. I feel, however, that the great reduction of number of known species of *Anisotarsus* from Central America is due rather to lack of adaptation to tropical environments. A total of 7 species of the subgenus *Notiobia* are recorded from this area. The species of both *Anisotarsus* and *Notiobia* tend to be found under debris on the ground, and if *Anisotarsus* species were numerous in Central America they should have been collected along with *Notiobia*. I personally have collected in Costa Rica, primarily in the lowlands, but did not encounter any *Anisotarsus* there.

Table 8 (p. 445) provides a list of the range extent determined for each species by a linear measurement between the 2 most distant localities on its distribution map. Thirty-one percent of the species have range extents less than 501 miles; 23 percent have ranges less than 1,001 miles; 31 percent have ranges of 1,001 to 2,000 miles; and 15 percent have ranges greater than 2,000 miles.

Ball and Freitag (in Freitag, 1969) and Erwin (1970) attempted by correlating species distributions to define centers of concentration for use in conjunction with a discussion of historical zoogeography of the species of their respective groups. To do this, Ball and Freitag, working on *Evarthrus*, which are flightless, excluded wide ranging species and those found on both sides of major barriers. Erwin working on the less barrier restricted *Brachinus*, which do fly, excluded species with ranges of over 1,000 miles. Since most species of *Anisotarsus* fly and are less barrier restricted than *Evarthrus*, I chose to follow Erwin and exclude species with ranges over 1,000 miles. This eliminated southern Texas as a possible center of concentration since the high number of species found there is primarily due to the overlapping of edges of widespread species. Also it eliminated the eastern United States.

Only 1 center of concentration can be delimited for *Anisotarsus* in North America. This is in central Mexico and contains 5 species with ranges less than 1,000 miles. In contrast, Ball and Freitag found *Evarthrus* has 8 centers of concentration, all in the eastern United States, while Erwin concluded that *Brachinus* has 8 in North and Central America combined. The absence of further centers of concentration in *Anisotarsus* is due in part to the smaller size of this group and in part to past species extinctions which have obscured centers of evolution.

Historical Zoogeography of the Subgenus *Anisotarsus*.

Since fossils are not known for this group, conclusions must be drawn from analyses of current distribution patterns of species, of the likely phylogeny of the group, and of information concerning past fluctuations in climate and flora. Because South American and Australian Region forms are not well known, this section deals mainly with the species of North America. The following sources have been consulted: Auffenberg and Milstead (1965); Axelrod (1948, 1958, 1959, 1967); Ball (1964, 1966); Ball and Freitag (in Freitag, 1969); Blair (1958, 1965); Darlington (1965); Dietz and Holden (1970); Dorf (1960); Erwin (1970); Graham (1964); Hopkins (1967); Howden (1969); King (1958); Larson (1969); MacGinitie (1958); Martin (1958); Martin and Mehringer (1965); Raven (1967);

Ross (1965); Smith and Hallam, (1970); Whitehead (1965); Wolfe (1969); and Wolfe and Leopold (1967).

In the early or middle Tertiary a species of *Anisotarsus* dispersed to North America by crossing water gaps between various islands in the present Central American and Caribbean areas. This species ultimately produced all of the North American *Anisotarsus* fauna except those of the *mexicana* lineage. This early crossing into North America is strongly suggested by the fact that except for the *mexicana* lineage the North and South American species of *Anisotarsus* do not show any close phylogenetic relationships.

The *mexicana* lineage is composed of 4 named forms. Three of these, *lamprota*, *chalcites*, and *amethystina*, seem to be adapted to or at least tolerant of tropical conditions although further field collecting and work needs to be done to verify this conclusion. The fourth form, *mexicana*, is adapted to mainly temperate or warm temperate conditions but extends far into Central America along mountains and highlands. The *mexicana* lineage is the only lineage common to both North and South America, its forms are all closely related, and 3 of its forms have tropical adaptations or tolerances. These facts suggest that the ancestor of the North American forms migrated north into North America via Central America after this area connected North and South America in the Pliocene. It is not probable that this migration took place earlier in the Tertiary because the *mexicana* lineage has several apomorphic characteristics suggesting recent evolution. And, the North and South American species undoubtedly would have diverged and lost their close relationship if isolated in the 2 continents earlier in the Tertiary before land connections were established.

It is difficult to reconstruct in detail the past zoogeographic history of the remaining North American *Anisotarsus*. The most productive approach is to determine the past history of individual species, groups of related species, and groups of species with similar contemporary distribution patterns.

The postulated phylogeny for New World *Anisotarsus* suggests that initial production of North American forms took place somewhere in Mexico. The species *brevicollis* is today centered in temperate and warm temperate Mexico and extends north into the southwestern United States. It is the sole extant member of the *brevicollis* lineage, which has no apparent synapomorphies with other lineages. On the basis of chorology its closest relative appears to be the *cyanippa* lineage which is restricted to central Mexico.

The *cyanippa* lineage is composed of the sister species *hilariola* and *cyanippa*, with the flightless *hilariola* known only from the vicinity of Chilpancingo and Omiltemi in Guerrero, and the usually flightless *cyanippa* recorded only from Jalisco, Morelos, and Nayarit. Since the 2 are closely related, and their ranges appear to be slightly disjunct, they probably arose from a common ancestor whose range in central Mexico was contracted by events during the Pleistocene.

The sister species *nitidipennis* and *schlingeri* show north-south vicariance, with *nitidipennis* occurring in the United States and Canada, and *schlingeri* being found in central Mexico. Presumably they had a common ancestor whose range was split into north and south components by Pleistocene events. The northern component became adapted to temperate conditions and gave rise to *nitidipennis* while the southern component became adapted to warm temperate conditions and produced *schlingeri*.

The species *virescens* and *picea* do not show close relationships to other species and little can be deduced about their past history except that their close relatives are now extinct.

The species *flebilis*, *purpurascens*, *mexicana* and *brevicollis* each have a disjunct distribution best explained by events of the Pliocene and Pleistocene. The species *flebilis* is restricted to Guadalupe Island, southern Baja California, and the Mazatlan region of western Mexico. The species *purpurascens* is found in coastal and highland areas of California, in

mountains surrounded by desert in Arizona, and in areas of various altitudes in Mexico and along the Gulf in southern United States. And *mexicana* and *brevicollis* are both centered in mainland Mexico but have disjunct populations in desert isolated mountains of Arizona, New Mexico, and southern Baja California.

The following climatic, floral, and geological events serve to explain the disjunct distributions of these 4 species. During Miocene and early Pliocene, Madro-Tertiary woodland and chaparral ranged widely over the lowlands of western United States, Baja California, and into Mexico (Axelrod, 1948, 1958, 1963). In late Pliocene and Pleistocene, the major mountain systems of North America, including the Sierra Nevada, Coastal Ranges of California, Transverse and Peninsular Ranges of California, Cascades of Oregon and Washington, Basin Ranges of Nevada, central and southern Rockies, and the Sierra Madres of Mexico, assumed their present heights (Axelrod, 1958). Volcanic activity in late Miocene formed a series of volcanoes extending along the present east coast of Baja California from the southern San Pedro Martirs in the north to the Cape Region at the south (Axelrod, 1958). These geological events were accompanied by, and in part produced, a continued decrease in yearly rainfall over lowland areas, a shift in the western United States and northwestern Mexico to a seasonal distribution of rain mainly in the winter, general lowering of winter temperature, and greater extremes of temperature (Axelrod, 1948, 1958, 1963, 1967).

The elevation of the Sierra Nevada-Cascade axis and the Peninsula Ranges of southern California along with decreased yearly rainfall produced drier inland climates, and the present desert climax evolved in dry areas of the American southwest. This increasing aridity and desert development during late Pliocene and Pleistocene isolated more mesic plant formations such as woodland on the higher summits of Guadalupe Island, and mountainous areas of Baja California, Arizona, and New Mexico. Today the Guadalupe Island flora contains 164 native vascular plant species, of which 32 are endemic to the island and 24 to this island and the southern California Islands (Raven, 1967). The Sierra Laguna south of La Paz and to a lesser degree the higher parts of the Sierra Gigantea in southern Baja today contain a distinctive woodland termed "Lagunan Woodland" by Axelrod (1958). Many of the late Tertiary fossil plant species of this woodland also occurred at that time in the southwestern United States. Today many of the extant species are endemic while some occur also in the mountains of southern Sonora and Sinaloa (Axelrod, 1958). The Lagunan Woodland is a distinctive derived assemblage of the broader Sierra Madrean Woodland which today ranges across north Mexico from Southern Baja California to the Sierra Madre Oriental in Nuevo Leon and Tamaulipas and northward into southern Arizona, New Mexico and western Texas (Axelrod, 1958).

From the above information on late Tertiary and Pleistocene events, one might infer that *flebilis*, *purpurascens*, *brevicollis*, and *mexicana* were once more widespread over southwestern North America, but then retreated into Mexico and into island and mountain refugia elsewhere with the occurrence of increasing aridity during late Pliocene and early Pleistocene. However, the disjunct populations of these species are little differentiated, and if they had been isolated since late Pliocene or early Pleistocene, they might be more distinct. Desert areas of the southwestern United States were contracted during the ice ages of the Pleistocene. During the maximum ice advance of the Wisconsin period about 20,000 years ago, biotic zone depressions of 900 to 1,200 meters occurred in the southwestern United States, and woodland occupied lowlands in this area which is now again covered by desert or grassland (Martin and Mehringer, 1965). California and Baja California also experienced more mesic conditions and range extensions of woodland flora during Pleistocene glaciations (Axelrod, 1967). Thus, although the 2 species were probably isolated in

their refugia by late Pliocene or early Pleistocene, they presumably were able to spread over lowlands connecting these refugia as recently as the Wisconsin. This explains the lack of divergence of their now disjunct populations.

The species *terminata* contains 4 morphs which while intergrading over broad areas are each centered in distinct geographical areas. The northern, Texas, Florida, and Mexico morphs are respectively centered in: northern North America primarily north of the fortieth parallel; Texas; Florida; and Mexico. The occurrence of these morphs may be explained by Pleistocene events. The northern morph now occurs predominantly in areas with cool temperate climate, and most of the range it now occupies was covered by ice during the maximum Wisconsin ice advance (Howden, 1969). The part of its range not covered by ice at that time appears to have consisted of tundra and taiga or the northern boundary of a boreal forest (Martin, 1958). The northern morph thus has apparently occupied its present range only since Wisconsin.

There have been at least 3 additional earlier glacial periods during the Pleistocene (Howden, 1969). Possibly one or more of these glacial periods pushed populations of *terminata* south and westward and maintained them in a semi-isolated state in areas of the central United States (possibly the southern edge of the present Great Plains). These populations could then have evolved into the present northern morph.

Considerable controversy exists as to the degree of climatic change induced in the southern United States during the Wisconsin and other glacial periods. However, most workers are able to agree that there was at least some change. It is likely that the Wisconsin and almost certainly the 3 earlier glacial periods produced sufficient cooling to force populations of *terminata* into semi-isolated refugia in Florida, northern Mexico, and central or southern Mexico. There is considerable evidence of Floridian and Mexican refugia in other groups of insects (Howden, 1969) and in amphibians (Blair, 1965). The exact location of the presumed central or southern Mexico refugium and the reasons for its postulated semi-isolation cannot be determined until more is known about Pleistocene events in Mexico. Presumably during their periods of semi-isolation, the refugia produced the 4 morphs now found in *terminata*. When the ice ages ended, the morphs then moved into their present ranges.

The postulated central United States refugium produced the northern morph, the Florida refugium the Florida morph, the northern Mexico refugium the Texas morph, and the central or south Mexico refugium the Mexico morph. There is a possibility that the postulated northern Mexico refugium producing the Texas morph might have been located in southern California, Arizona, New Mexico or other areas of southwestern America. However, if this were so, then there would probably be disjunct populations of *terminata* in the mountains of these states. Also the possession of a slender median lobe by the Texas and Florida morphs suggests that the Florida refugium and the one producing the Texas morph were in contact during at least part of their existence. The probable way such contact took place was that the refugium producing the Texas morph was located in northern Mexico and connected to the Florida one by a narrow Gulf Coast corridor. The tendency for the median lobe of Mexico morph specimens to broaden southwards suggests that the refugium producing this morph may have been more isolated from the Florida and northern Mexico ones. However, I do not presently know what climatic or environmental conditions in Mexico could have produced such isolation.

Only 1 center of concentration can today be delimited for *Anisotarsus* in North America, and it occurs in central Mexico. Considerable evolution may have occurred there during late Tertiary and Pleistocene. However, before early Oligocene much of Mexico and southern United States had a tropical climate (Dorf, 1960), and most evolution before then probably

took place in more northern localities.

The eastern United States today contains 5 species, *purpurascens*, *terminata*, *nitidipennis*, *picea*, and *maculicornis*. The first species extends no farther north than the Gulf region and is centered mainly in Mexico. The species *terminata*, *nitidipennis*, and *picea* are widespread forms with range extents over 1,000 miles and each extend northward to or slightly beyond the forty-fifth parallel. The species *maculicornis* has a range extent of 750 miles and is more numerous and primarily concentrated around the Gulf region and associated lowlands. The distribution of species in the eastern United States and Canada suggests that the maximum periods of Pleistocene glaciation had a devastating effect on *Anisotarsus* of these 2 areas and pushed species south or southwest or exterminated them. It is reasonable to postulate that if maximum glacial periods had not had such a devastating effect, then the unglaciated areas of the eastern United States would have several localized species as does Mexico. The species *terminata*, *nitidipennis*, and *picea* appear to be vagile forms which have only recently spread northward from possible southern refugia or centers of evolution. And *maculicornis* may also be a species now extending its range northward.

The species of *Anisotarsus* in the Australian Region are little differentiated from those in the New World. Australia and Antarctica were connected until some time in Tertiary (Dietz and Holden, 1970; Smith and Hallam, 1970). And from late Cretaceous to Miocene, *Nothofagus* and certain other plants occurred on the present day Antarctica Peninsula and possibly elsewhere on the continent (Darlington, 1965). The juncture of Australia and Antarctica and the presence of plants at least on the Antarctica Peninsula suggest that *Anisotarsus* could easily have dispersed to Australia as recently as Eocene or early Miocene. This would account for the similarity of species of the Australian Region and New World.

Zoogeography of the Subgenus *Notiobia*.

A detailed discussion of the zoogeography of the species of *Notiobia* (*s. str.*) is not possible until more is known about the Central and South American forms; a few general comments will be made here. The subgenus is Neotropical (Fig. 146) with its species apparently confined to tropical areas. A few Mexican species extend into areas such as montane cloud forests which might be classified as subtropical rather than tropical. The subgenus may have 3 centers of concentration: southern Mexico with 9 species, 6 of which extend south into Central or South America; Central America which has probably 10 or more species, some of which extend into Mexico or South America; and South America which probably contains more than 20 species. In Figure 146 much of the interior of Brazil and northern South America lacks dots indicating presence of *Notiobia* (*s. str.*). I have seen specimens at various museums from these interior regions but have not recorded the exact localities of such specimens. This will be done in a forthcoming revision of the Central and South American species of the subgenus *Notiobia*.

Contemporary Zoogeography of the Subgenus *Gynandrotarsus*.

Climatological data used to explain current distributions are taken from the 1941 Yearbook of Agriculture and Leopold (1959). The distribution of each of the 10 species is shown by dots on separate maps (Figs. 157-166). In Fig. 254 the ranges of all the species are each delimited by a line drawn around the outermost dots for each species. The circles shown in Fig. 254 depict widely disjunct collections each based on a single known specimen of: *opaculus* from Yuma, Arizona; *merula* from Anaheim, California; *dulcicollis* from Los Angeles County, California and from the Huachuca Mountains of Arizona. Since these disjunct collections occur in fairly well collected areas far removed from the species main range, the specimen in question of each species may have been mislabeled.

Figures 157-166 and 254 indicate that species of *Gynandrotarsus* are most numerous in the south central United States (in an area between approximately the thirtieth and fortieth parallels and the ninetieth and one hundredth meridians), and in the United States east of the Mississippi River as 7 species are found in each area. Mexico is strikingly poor in number of species with only *anthracinus* and *darlingtoni* being centered there and *texanus* and *opaculus* extending slightly into it. Florida is also poor in number of species with only *merula* and *haplomus* being widespread there and *rusticus* currently being known only from the Jacksonville area in the extreme northeastern part of the state. The western United States today contains only the single specimens representing the disjunct collections described above and western or northern extensions of species primarily centered in Mexico, east central, or eastern United States. Northern areas also contain few species. Only 3 species are found north of the Canadian border. These 3 are all wide ranging forms primarily centered in more southern latitudes and extend only into the southeastern part of Canada.

It is likely that species of *Gynandrotarsus* are primarily adapted to those temperate and warm temperate environments that receive summer rainfall. The low number of species in Mexico and Florida is possibly explained by lack of tolerance to environments that are warm and humid throughout the year. Also, species found in Mexico are primarily restricted to highland areas receiving frost during the winter. In Florida only *merula* and possibly *haplomus* extend into relatively frost free zones. The decrease in number of species westward seems correlated with decreasing summer rainfall. The decrease in number of species northward is probably due to a lack of tolerance for cold and also in part to the effects of Pleistocene glaciation (see Howden, 1969).

The species distributions have limited correlation with topography. Species found in Mexico are primarily restricted to highland regions which have cooler climates. The species *anthracinus*, which is found in Mexico and the southwestern United States, is in the United States primarily associated with mountainous areas or the foothills of such areas. This pattern probably results from the desert barrier surrounding such elevated areas. In the warm temperate eastern United States, species range over mountains and rivers which are often barriers to other groups of Carabidae (such as the genus *Evarthrus*, Ball and Freitag, in Freitag, 1969).

Table 9 (p. 446) lists the range extents for each species, as determined by a linear measurement between the 2 most distant localities on each species distribution map. (The single specimens representing the disjunct localities of *merula*, *opaculus*, and *dulcicollis* were omitted in range extents determinations. No species have a range extent of less than 500 miles; 30 percent of the species have range extents of 501 to 1,000 miles; 40 percent have range extents of 1,001 to 1,500 miles; 20 percent have range extents of 1,501 to 2,000 miles; and 20 percent have range extents of 2,001 or more miles.

As discussed in detail in the section on contemporary zoogeography of the species of *Anisotarsus*, Ball and Freitag (in Freitag, 1969) and Erwin (1970) attempted by correlating species distributions to define the centers of species concentration. These centers served as data for a discussion of the historical zoogeography of the species of their respective groups. I have done this for *Anisotarsus*; following Erwin, I excluded all species with range extents of over 1,000 miles in my determination of the centers of concentration for this subgenus. On the average, the species of *Gynandrotarsus* are more vagile than those of *Anisotarsus*, and using the 1,000 mile limit would exclude all but 3 species. Therefore, for *Gynandrotarsus* I exclude only those species with range extents of more than 1,500 miles. When this is done, the area between approximately the thirtieth and fortieth parallels and the ninetieth and one hundredth meridians of the south central United States becomes the only center of concentration. It contains 6 of the 10 *Gynandrotarsus* species: *harpaloides*, *opacu-*

hus, *texanus*, *dulcicollis*, *ovularis*, and *haplomus*. The single remaining species with a range extent of less than 1,500 miles is *darlingtoni* which is known only from central and northern Mexico. The eastern United States is eliminated as a center of concentration since most of the species found there either have range extents greater than 1,500 miles or are merely extreme eastern extensions of species centered in the south central area described above. The absence of other centers of concentration for *Gynandrotarsus* is perhaps due to the small size of this group, to the high vagility of species, and to extinctions which now obscure the actual centers of evolution.

Historical Zoogeography of the Subgenus *Gynandrotarsus*.

The ancestor of *Gynandrotarsus* most likely crossed into eastern North America during late Cretaceous or early Paleocene via the connection with the European part of Eurasia (Fig. 252). Much of North America had a warm or tropical climate in early Tertiary (Axelrod, 1958; Dorf 1960). Extant species of *Gynandrotarsus* are not adapted to a warm climate, and crossing probably took place along the northern portions of the eastern North America-Eurasia connection. Initial evolution in eastern North America also probably occurred in areas of Alaska, Canada, and the northern United States which today lack species of *Gynandrotarsus*.

The 4 species of the sister *harpalooides* and *texanus* lineages are all centered in the south central United States. This suggests that the evolution of these 2 lineages from a common ancestral stock occurred there. Since this area had a tropical or very warm climate before early Oligocene (Dorf, 1960), such evolution probably did not occur until Oligocene or later.

The sister species of the *harpalooides* lineage have a degree of spatial and ecological vicariance. The species *harpalooides* is found (Fig. 159) in the central United States and apparently extends no farther south than northern Texas and northern Louisiana. And *opaculus* occurs (Fig. 158) in the central United States and extends south into northern Mexico. The limited ecological data available suggest that *opaculus* may occur primarily in, or have greater tolerance to, semi-arid conditions such as scrub desert; and possibly *harpalooides* is restricted to more mesic areas. If *opaculus* occurs in both mesic and semi-arid areas and *harpalooides* in mesic areas, then the 2 species have probably been in existence long enough to develop mechanisms enabling them to coexist in the same ecological zone. If *opaculus* is restricted to arid regions and *harpalooides* to mesic areas, then probably the 2 species have not been in existence long enough to successfully invade each other's ecological zones. Also *opaculus* possesses prominent dorsal microsculpture while *harpalooides* and the 2 species of the *texanus* lineage have reduced dorsal microsculpture. This suggests that *opaculus* is the end product of a series of species evolving from the *harpalooides* stock if reduced dorsal microsculpture is regarded as plesiomorphic for the *harpalooides* and *texanus* lineages. If reduced dorsal microsculpture is apomorphic, then *opaculus* is either relatively old or else a species simply retaining a plesiomorphic character state. As discussed in the section on phylogeny, *opaculus* is the closest relative of *harpalooides*. In the absence of additional information, *harpalooides* and *opaculus* probably evolved during the climatic changes of the late Pliocene or early Pleistocene.

The ranges (Figs. 164, 165) of the sister species *texanus* and *dulcicollis* of the *texanus* lineage overlap in Texas, but *texanus* is found only in the southern part of the United States and in northern Mexico while *dulcicollis* is found not only in the south but also as far north as Nebraska, Iowa, and Ohio. The two species thus have at least limited spatial vicariance. They also have a degree of ecological vicariance since available data indicate that *texanus* is restricted to dry semi-desert environments while *dulcicollis* is found in more mesic environ-

ments such as green pastures, orchards, cultivated lands, and grassy areas. These spatial and ecological vicariances suggest that the 2 species arose relatively recently from a common ancestor; *texanus* is found in arid semi-desert regions which likely did not evolve until late Pliocene-early Pleistocene (Axelrod, 1948, 1958, 1963, 1967), and these 2 species probably therefore evolved in late Pliocene or early Pleistocene.

The species *haplomus* belongs to a monotypic branch, has several apomorphic features unique in *Gynandrotarsus*, and is not closely related to other extant species. The unique apomorphic features suggest it evolved before the Pleistocene, but since *haplomus* has a range (Fig. 166) extending across much of the United States, its place of origin can not be elucidated.

The species *rusticus* belongs to a monotypic lineage, is not closely related to other extant species, and occurs (Fig. 162) across all of the eastern United States and in southeastern Canada. Its place and time of origin can not be elucidated without further data.

The species *merula* and *anthracinus* which are closely related on morphological grounds exhibit spatial vicariance: *merula* is found (Fig. 161) in southeastern Canada and in the eastern United States as far west as central Texas; *anthracinus* is found (Fig. 160) in the Davis Mountains of extreme southwestern Texas, mountainous or elevated areas of New Mexico, Arizona, possibly California, and in the highlands of northern and central Mexico. The 2 species have limited ecological vicariance, with *anthracinus* presumably adapted to warmer and possibly more arid environments. Their morphological features and their spatial and possible ecological vicariance suggest that these 2 species have only recently evolved from a common ancestor. Most likely, increasing aridity during Pliocene split the range of their common ancestor into northern and southern components.

The populations of *anthracinus* in the southwestern United States are separated by desert. Despite this, the populations associated with various mountainous or elevated areas exhibit no apparent differentiation. This may be due partly to the vagility of this species, but I feel past Pleistocene climatic changes are the main cause of this lack of differentiation. During Pleistocene glacial periods, desert areas of the United States were contracted, and populations of *anthracinus* were thereby brought into contact with each other. The last period of such contact occurred approximately 20,000 years ago during the maximum ice advance of the Wisconsin. At this time, biotic zone depressions of 900 to 1,200 meters occurred in the southwestern United States, and woodland then occupied lowlands now covered by desert or grassland (Martin and Mehringer, 1965). At this time, and also during earlier ice ages, populations of *anthracinus* moved down from mountainous or elevated areas and occupied all present desert areas.

The apparent absence of *darlingtoni* from mountainous and elevated areas of the southwestern United States which contain refugial populations of *anthracinus* and of other carabids suggests that *darlingtoni* evolved in Mexico and was never present in the United States. The time of its evolution cannot be elucidated without further data. The species *ovularis* is centered in the plains area of the United States (Fig. 163) and possibly evolved there as a result of floral shifts induced by Pleistocene climatic changes.

Only 1 center of concentration can be determined for *Gynandrotarsus*, in the south central United States. Before early Oligocene this area had a tropical or warm climate (Dorf, 1960), and earlier evolution of *Gynandrotarsus* probably took place in more northern localities. However, after early Oligocene, considerable evolution of species occurred in the south central United States; four species of the *texanus* and *harpaloides* lineages seem to have evolved there. The species *merula* extends into the south central center of concentration while its sister species *anthracinus* is found to the west and southwest. Possibly, the common ancestor of these 2 species occupied at least part of the present center of concen-

tration and also extended west and south into the present range of *anthracinus*. Presumably, Pliocene events subsequently divided the range of this species, thus allowing evolution of *anthracinus* and *merula*.

Today there are 7 species in the United States east of the ninetieth parallel. Two of these, *harpaloides* and *opaculus*, are centered in the south central United States. The species *ovularis* is widespread with a range extent of 1,500 miles, is found only as far south as approximately the thirty-fifth parallel, and is centered in the north central grasslands of the United States. The remaining 4 species, *haplomus*, *rusticus*, *merula*, and *dulcicollis* all have range extents of more than 1,400 miles and are most concentrated or abundant in central or southern latitudes of the United States. The distribution of species in the eastern United States suggests that the maximum periods of Pleistocene glaciations had a devastating effect on most of the then extant species, pushing them south or southwest or exterminating them. If maximum glacial periods had not produced such a drastic effect, then the unglaciated areas of the eastern United States would probably have several more localized species as does the south central United States. The species *rusticus*, *merula*, *dulcicollis*, and *haplomus*, are vagile forms which may only recently have spread northward from possible southern refugia or centers of evolution.

ACKNOWLEDGEMENTS

I wish to express my deep gratitude to Evert I. Schlinger, my former major professor, who offered continued assistance and encouragement during the course of research for this paper. Also I wish to thank both him and his wife Audrey Schlinger for providing hospitality and lodging during part of this study.

Special thanks are due to: George E. Ball, Kenneth Cooper, William Ewart, P.J. Darlington, Jr., Carl H. Lindroth, and Paul Spangler who kindly offered advice and assistance during the course of this study.

I am grateful to Paul Spangler and his wife Phyllis Spangler who did much to make a 1 year visit at the Smithsonian Institution both very productive and enjoyable.

George Ball, P.J. Darlington, Jr., and Carl Lindroth suggested this study, and I thank them for their advice. Robin Clarke kindly provided useful information on several African taxa.

Publication of this paper was made possible by funds supplied by G. E. Ball from his NRC grant A-1399. Most of the Mexican specimens studied for this paper were collected by G. E. Ball during trips financed by his NSF grant GB-3312; revision of the North American species of *Notiobia* and *Gynandrotarsus* would have been impossible without these Mexican specimens.

Several people and institutions provided funds making this study possible, and I wish to express my gratitude for this assistance. The University of California at Riverside supplied stipend and research funds during the first 2 years of this study. The Smithsonian Institution provided a stipend and research funds making possible a year's visit at this institution and partly financing a trip to European museums. The Society of the Sigma Xi gave funds which partly defrayed expenses of the trip to European museums. P.J. Darlington, Jr. kindly made available funds from the Museum of Comparative Zoology so that I could visit him and work on specimens at the museum. The Field Museum of Natural History, through the Karl P. Schmidt Memorial Fund, made it possible for me to visit the museum and examine specimens there. The University of California at Berkeley made available a fellowship which supported me during the writing of certain sections of this paper. And the University of Alberta provided me with financial support and technical assistance during

the production of the final manuscript of this paper.

I am grateful to the following people for reading and editing all or portions of this paper: George E. Ball, Kenneth Cooper, Terry Erwin, William Ewart, Evert Schlinger, and Donald R. Whitehead. Kenneth Cooper tested the species keys, and George Ball tested the superspecific keys.

John S. Scott prepared many of the illustrations in this paper, and I thank him for his valuable assistance. Natalie Daviduk and Linda Meissenheimer kindly typed the final manuscript copy.

I wish to thank the following curators for hospitality shown me during visits to their museums: Madame A. Bons, Museum National d'Histoire Naturelle, Paris, France; John Chemsak, California Insect Survey, University of California at Berkeley; P.J. Darlington, Jr., Museum of Comparative Zoology, Harvard University; Henry Dybas and Rupert Wenzel, Field Museum of Natural History; Peter Hammond, British Museum of Natural History, London, England; Hugh B. Leech, California Academy of Sciences; Carl H. Lindroth, Zoological Institute, Lund, Sweden; and Paul Spangler, United States National Museum, Smithsonian Institution.

Special thanks are due J. Nègre for hospitality during my visit to the Paris Museum and for allowing me the privilege of examining his extensive carabid collection and library.

The following persons and curators kindly loaned me specimens during the course of this study: R.D. Alexander, The University of Michigan, Ann Arbor, Michigan 48104; George E. Ball, The University of Alberta, Edmonton, Alberta, T6G 2E3, Canada; W.F. Barr, University of Idaho, Moscow, Idaho 83843; Edward C. Becker, Canadian National Collection, Canada Department of Agriculture, Entomology Research Institute, Central Experimental Farm, Ottawa, Ontario, Canada; Madame A. Bons, Museum National d'Histoire Naturelle, 45 bis rue de Buffon, Paris (V), France; Horace R. Burke, Texas A and M University, College Station, Texas 77843; Bobie T. Chapin, Louisiana State University, Baton Rouge, Louisiana 70803; John Chemsak, California Insect Survey, University of California, Berkeley, California 94720; P.J. Darlington, Jr., Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02128; William Drew, Oklahoma State University, Stillwater, Oklahoma 74074; Terry Erwin, United States National Museum, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; Roland Fischer, Michigan State University, East Lansing, Michigan 48823; Hiliary Hacker, 235 Randall Street, San Francisco, California 94131; Peter Hammond, British Museum (Natural History), London S.W. 7, England; Lee H. Herman, Jr., American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024; Charles Hogue and Roy Snelling, Los Angeles County Museum of Natural History, Exposition Park, Los Angeles, California; Dave Larson, University of Calgary, Calgary 44, Alberta, Canada; Hugh B. Leech, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118; W. Wayne Moss, Academy of Natural Sciences, Philadelphia, Pennsylvania 19103; Paul Oman, Oregon State University, Corvallis, Oregon 97331; L.L. Pechuman, Cornell University, Ithaca, New York 14850; E. P. Rouse and R.T. Allen, University of Arkansas, Fayetteville, Arkansas; Robert D. Schuster, University of California, Davis, California 95616; Milton W. Sanderson, Illinois Natural History Survey, Urbana, Illinois 61801; Paul J. Spangler, United States National Museum, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; Rupert L. Wenzel and H. Dybas, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605; Robert E. Woodruff, Florida Department of Agriculture and Consumer Services, Bureau of Entomology, P.O. Box 1269, Gainesville, Florida, 32601.

LITERATURE CITED

Agassiz, J. L. R. 1846. Nomenclatoris zoologici. Index universalis, continens nomina systematica classium, ordinum, familiarum et generum animalium omnium, tam viventium quam fossilium, secundum ordinem alphabeticum unicum disposita, adjectis, homonymiis planatarum, nec non variis adnotationibus et emendationibus. Soloduri. 393 p.

Andrewes, H. E. 1919. Papers on Oriental Carabidae I. Ann. Mag. nat. Hist. Ser. 9, 3: 469-483.

Andrewes, H. E. 1929. Papers on Oriental Carabidae XII. Ann. Mag. nat. Hist. Ser. 10, 4: 353-371.

Andrewes, H. E. 1933. Papers on Oriental Carabidae. XXVII. Ann. Mag. nat. Hist. Ser. 10, 11: 99-110.

Antoine, M. 1959. Coléoptères carabiques du Maroc. Troisième partie. Mem. Soc. Sci. nat. phys. Maroc. Nouvelle Série, 6: 315-465.

Ashlock, P. D. 1971. Monophyly and associated terms. Syst. Zool. 20 (1): 63-69.

Auffenberg, W. and W. W. Milstead. 1965. Reptiles in the Quaternary of North America. p. 557-568. In H. E. Wright, and D. G. Frey (ed.). The Quaternary of the United States. Princeton University Press, New Jersey.

Axelrod, D. I. 1948. Climate and evolution in western North America during middle Pliocene time. Evolution. 2: 127-144.

Axelrod, D. I. 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev. 24 (7): 433-509.

Axelrod, D. I. 1959. Geological history. p. 5-9. In P. A. Munz and D. D. Keck, A California Flora. University of California Press, Los Angeles.

Axelrod, D. I. 1963. Geological history. p. 5-9. In P. A. Munz and D. D. Keck, A California Flora, second edition. University of California Press, Los Angeles.

Axelrod, D. I. 1967. Geologic history of the Californian Insular Flora. p. 267-315. In R. N. Philbrick (ed.), Proceedings of the Symposium on the Biology of the California Islands. Santa Barbara Botanic Garden, Santa Barbara, California.

Ball, G. E. 1956. Notes on the genus *Zacotus* LeConte, 1869, and on the classification of the tribe Broscini (=Broscidae sensu Jeannel, 1941. Coleoptera, Carabidae). Coleop. Bull. 10 (3): 33-52.

Ball, G. E. 1960a. Carabidae (Latreille, 1810). p. 55-181. In R. H. Arnett Jr., The Beetles of the United States. The Catholic University of America Press, Washington, D. C. [published together with other material as part I of this book].

Ball, G. E. 1960b. A review of the taxonomy of the genus *Euryderus* LeConte, 1848. With notes on the North American Dapti (of authors) (Carabidae: Harpalini). Coleop. Bull. 14: 44-64.

Ball, G. E. 1963. Carabidae (Latreille, 1810). p. 55-181. In R. H. Arnett, Jr., The Beetles of the United States. The Catholic University of America Press, Washington, D. C. [bound book consisting of previously published parts].

Ball, G. E. 1964. Relationships of certain populations of ground beetles in southern Arizona. p. 253-255. In Yearbook of the American Philosophical Society.

Ball, G. E. 1966. The taxonomy of the subgenus *Scaphinotus* Dejean with particular reference to the subspecies of *Scaphinotus petersi* Roeschke (Coleoptera: Carabidae: Cychrini). Trans. Am. ent. Soc. 92: 687-722.

Ball, G. E. 1970. The species of the Mexican genus *Azetecarpalus*, new genus (Coleoptera: Carabidae: Harpalini). Coleop. Bull. 24 (4): 97-123.

Ball, G. E. and T. L. Erwin. 1969. A taxonomic synopsis of the tribe Loricerini (Coleoptera: Carabidae). Can. J. Zool. 47 (5): 877-907.

Ball, G. E. and R. Freitag. 1969. Zoogeography. p. 174-190. In R. Freitag, A revision of the species of the genus *Evarthrus* LeConte (Coleoptera: Carabidae). *Quaest. ent.* 5: 89-212.

Basilewsky, P. 1946a. Étude des Coléoptères Carabidae Africains des collections du Naturhistoriska Riksmuseum de Stockholm. *Ark. Zool.* 38a (18): 1-20.

Basilewsky, P. 1946b. Coléoptères Harpalides Africains nouveaux du Muséum d'Histoire Naturelle de Paris. *Revue fr. Ent.* 13 (4): 168-185.

Basilewsky, P. 1948. Carabidae Africains nouveaux I. *Mem. Soc. r. ent. Belg.* 57-105.

Basilewsky, P. 1950. Révision générale des Harpalinae d'Afrique et de Madagascar (Coleoptera: Carabidae), Part 1. *Annls. Mus. r. Congo belge Ser.* 8, 6: 283 p., 9 pls.

Basilewsky, P. 1951. Révision générale des Harpalinae d'Afrique et de Madagascar (Coleoptera: Carabidae), Part 2. *Annls. Mus. r. Congo belge Ser.* 8, 9: 333 p., 6 pls.

Bates, H. W. 1874. On the geodephagous Coleoptera of New Zealand. *Ann. Mag. nat. Hist. Ser.* 4, 13: 233-246, 270-277.

Bates, H. W. 1878a. On new genera and species of geodephagous Coleoptera from Central America. *Proc. zool. Soc. Lond.* 1878: 587-609.

Bates, H. W. 1878b. New genera and species of Carabidae from Tasmania. *Cistula Entomologica*, 2: 317-326.

Bates, H. W. 1882. *Biologia Centrali-Americanana, Insecta, Coleoptera, Carabidae.* vol. 1, pt. 1, p. 40-152, pls. iii-v.

Bates, H. W. 1884. *Biologia Centrali-Americanana, Insecta, Coleoptera, Cincindelidae suppl. Carabidae suppl.* vol. 1, pt. 1, p. 257-290, 13 pls.

Bates, H. W. 1891. Additions to the carabideous fauna of Mexico, with remarks on some of the species previously recorded. *Trans. ent. Soc. Lond.* 1891: 223-278.

Bedel, L. 1895. Catalogue raisonné des coléoptères du nord de l'Afrique (Maroc, Algérie, Tunisie et Tripolitaine) avec notes sur la faune des îles Canaries et de Madère, pt. 1. Société Entomologique de France, Paris, 320 p.

Blair, W. F. 1958. Distributional patterns of vertebrates in the southern United States in relation to past and present environments. p. 433-468. In C. L. Hubbs (ed.) *Zoogeography*. Publ. 51. American Association for the Advancement of Science, Washington, D. C.

Blair, W. G. 1965. Amphibian speciation. p. 543-556. In H. W. Wright and D. G. Frey (ed.), *The Quaternary of the United States*. Princeton University Press, New Jersey.

Blatchley, W. S. 1910. An illustrated descriptive catalogue of the Coleoptera or Beetles (Exclusive of the Rhynchophora) known to occur in Indiana, with bibliography and descriptions of new species. The Nature Publishing Co., Indianapolis. 1386 p.

Britton, E. B. 1949. The Carabidae (Coleoptera) of New Zealand. Part III-A revision of the tribe Broscini. *Trans. R. Soc. N. Z.* 77 (4): 533-581, pls. 59-78.

Broun, T. 1903. Descriptions of new genera and species of New Zealand Coleoptera. *Ann. Mag. nat. Hist. Ser.* 7, 11: 450-458, 602-618.

Brullé, G. A. 1838. Insectes de l'Amérique méridionale recueillis par Alcide d'Orbigny. p. 17-56. In *Voyage dans l'Amérique Méridionale . . . par Alcide d'Orbigny*, vol. 6, pt. 2, Insectes. Paris.

Brundin, L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges, with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. *K. svenska Vetensk. Akad. Handl.* (4) 11: 1-472.

Brundin, L. 1972. Phylogenetics and biogeography. *Syst. Zoo.* 21 (1): 69-79.

Carret, A. 1905. Description d'un nouveau carabide appartenant à la faune syrienne. *Bull. Soc. ent. Fr.* 1905: 122-124.

Casey, T. L. 1884. Contributions to the descriptive and systematic coleopterology of North America, pt. 1, 60 p.

Casey, T. L. 1914. A revision of the Nearctic Harpalinae. *Memoirs on the Coleoptera*. 5: 45-305.

Casey, T. L. 1918. Miscellaneous notes and corrections. *Memoirs on the Coleoptera*. 8: 413-416.

Casey, T. L. 1924. Additions to the known Coleoptera of North America. *Memoirs on the Coleoptera*. 11: 1-347.

Castelnau (de Laporte), F. L. N. C. 1867. Notes on Australian Coleoptera. *Trans. R. Soc. Vict.* 1867: 1-139.

Chaudoir, M. 1835. Description de quelques genres et espèces de carabiques nouveaux. *Annls. Soc. ent. Fr.* 4: 429-448.

Chaudoir, M. 1837. Genres nouveaux et espèces nouvelles de coléoptères de la famille des carabiques. *Moskovskoe Obschestvo Ispateleli Prirody*. 10 (7): 3-48.

Chaudoir, M. 1843a. Genres nouveaux de la famille des carabiques (continuation). *Moskovskoe Obschestvo Ispateleli Prirody*. 16 (3): 383-427.

Chaudoir, M. 1843b. Carabiques nouveaux. *Moskovskoe Obschestvo Ispateleli Prirody*. 16 (4): 671-791.

Chaudoir, M. 1854. Mémoire sur la famille des carabiques. *Moskovskoe Obschestvo Ispateleli Prirody*. 27 (2): 279-352.

Chaudoir, M. 1868. Observations synonymiques sur les carabiques de l'Amérique septentrionale et descriptions d'espèces nouvelles de ce pays. *Revue et Magasin de Zoologie Pure et Appliquée*, Ser. 2, 20: 161-171, 211-217, 239-245, 283-301, 331-345.

Chaudoir, M. 1878. Les harpaliens d'Australie d'après la collection de M. le Comte de Castelnau et la mienne. *Annali Mus. civ Stor. nat.* 12: 475-517.

Chevrolat, L. A. A. 1842. In C. D. d'Orbigny, *Dictionnaire universel d'histoire naturelle* ... vol. 2. C. Renard, Paris, 796 p.

Colless, D. H. 1972. A note on Ashlock's definition of "monophyly". *Syst. Zool.* 21: 126-128.

Crowson, R. A. 1955. The natural classification of the families of Coleoptera. [1967 reprint by E. W. Classey Ltd., Middlesex of 1955 book. 214 p.]

Csiki, E. 1932. *Coleopterorum Catalogus*, Pars 121. Carabidae: Harpalinae VI. W. Junk. Berlin. p. 1023-1278.

Curtis, J. 1839. Descriptions, &c. of the insects collected by Captain P. P. King, R. N. F. R. S. & L. S. in the survey of the Straits of Magellan. *Trans. Linn. Soc. Lond.* 18: 181-205, 1 pl.

Darlington, P. J., Jr. 1949. Beetles and continents. A review of La genèse des faunes terrestres: éléments de biogéographie. *Q. Rev. Biol.* 24 (4): 342-404.

Darlington, P. J., Jr. 1957. Zoogeography: the geographical distribution of animals, John Wiley & Sons, Inc., New York. 675 p.

Darlington, P. J., Jr. 1959. Area, climate and evolution. *Evolution*. 13: 488-510.

Darlington, P. J., Jr. 1965. Biogeography of the southern end of the world, distribution and history of far-southern life and land, with an assessment of continental drift. Harvard University Press, Cambridge. 236 p.

Darlington, P. J., Jr. 1968. The Carabid Beetles of New Guinea Part III. Harpalinae (continued): Perigonini to Pseudomorphini. *Bull. Mus. comp. Zool. Harv.* 137 (1): 1-253.

Darlington, P. J., Jr. 1970. A practical criticism of Hennig-Brundin "phylogenetic systematics" and Antarctic biogeography. *Syst. Zool.* 19 (1): 1-18.

Darlington, P. J., Jr. 1972. What is cladism? *Syst. Zool.* 21 (1): 128-129.

Darwin, C. 1856. The origin of species. [reprint of first edition, The Modern Library, New York.]

Dejean, P. F. M. A. 1829. Spécies général des coléoptères de la collection de M. le Comte Dejean, vol. 4. Méquignon-Marvis, Paris. 520 p.

Dejean, P. F. M. A. 1831. Spécies général des coléoptères de la collection de M. le Comte Dejean, vol. 5, pt. 2. Méquignon-Marvis, Paris. p. 385-883.

Dejean, P. F. M. A. 1837. Catalogue des coléoptères de la collection de M. le Comte Dejean. Troisième édition, revue, corrigée et augmentée. Méguignon-Marvis Pere et Fils, Paris. 503 p.

Dietz, R. S. and J. C. Holden. 1970. Reconstruction of Pangaea: break up and dispersion of continents, Permian to present. *J. geophys. Res.* 75 (26): 4939-4956.

Dorf, E. 1960. Climatic changes of the past and present. *Am. Scient.* 48 (3): 341-364.

Elliot, D. H., E. H. Colbert, W. J. Breed, J. A. Jensen and J. S. Powell. 1970. Triassic tetrapods from Antarctica: evidence for continental drift. *Science.* 169. 1197-1200.

van Emden, F. 1953. The Harpalini Genus *Anisotarsus* Dejean (Col. Carab.). *Ann. Mag. nat. Hist. Ser.* 12, 6: 513-547.

Erichson, W. F. 1837. Die Käfer der Mark Brandenburg. Erster Band, erste Abtheilung. F. H. Morin, Berlin. viii, 384 p.

Erichson, W. F. 1847. Conspectus Insectorum Coleopterorum, quae in Republica Peruanan observata sunt. *Arch Naturgesch.* 13: 67-185.

Erwin, T. L. 1970. A reclassification of bombardier beetles and a taxonomic revision of the North and Middle American species (Carabidae: Brachinida). *Quaest. ent.* 6 (4): 1-215.

Erwin, T. L. 1971. Fossil tachyine beetles from Mexican and Baltic amber, with notes on a new synonymy of an extant group (Col, Carabidae). *Ent. scand.* 2: 233-236.

Fooden, J. 1972. Breakup of Pangaea and isolation of relict mammals in Australia, South America and Madagascar. *Science* 175: 894-898.

Forbes, S. A. 1883. The food relations of the Carabidae and Coccinellidae. *Bull. Ill. St. Lab. nat. Hist.* 1 (6): 33-60.

Germar, E. F. 1824. Insectorum species novae aut minus cognitae, descriptionibus illustratae. vol. 1. Coleoptera. J. C. Hendelii et Filii, Halae. xxiv, 624 p., 2 pls.

Graham, A. 1964. Origin and evolution of the biota of southeastern North America: evidence from the fossil plant record. *Evolution* 18 (4): 571-585.

Griffiths, G. C. D. 1971. Studies on the phylogenetic classification of Diptera Cyclorrhapha, with special reference to the structure of the male postabdomen. Ph.D. Thesis, University of Alberta, Edmonton, Alberta. 298 p.

Guérin-Méneville, F. E. 1847. Insects. p. 239-390, 12 pls, *In* O. Murs, F. Prevost, Guichenot, and Guérin-Méneville, *Voyage en Abyssinie exécuté pendant les années 1839, 1840, 1841, 1842, 1843*. Arthus Bertrand, Paris.

Habu, A. 1955. On two species of Carabidae from Mt. Hiko (Coleoptera) (The Carabidae-fauna of Mt. Hiko, IV). *Insecta matsum.* 19 (1-2): 35-39.

Habu, A. 1973. Fauna Japonica. Carabidae: Harpalini (Insecta: Coleoptera). Keigaku Publishing Co., Ltd., Tokyo, Japan. xiii, 430 p., 14 pls.

Haldeman, S. S. 1843. Descriptions of North American species of Coleoptera, presumed to be undescribed. *Proc. Acad. nat. Sci. Philad.* 1: 298-304.

Heilprin, A. 1887. The geographical and geological distribution of animals. New York, Appleton. [I was unable to examine this work, and above title is from Darlington (1957)].

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana, Illinois. 263 p.

Hopkins, D. M. 1967. The Cenozoic history of Beringia--A synthesis. p. 451-484. *In* D. M. Hopkins (ed.), *The Bering Land Bridge*. Stanford University Press, Stanford, California.

Horn, G. H. 1881. On the genera of Carabidae with special reference to the fauna of Boreal America. *Trans. Am. ent. Soc.* 9 (1): 91-196, pls. 3-10.

Howden, H. F. 1969. Effects of the Pleistocene on North American insects. *A. Rev. Ent.* 14: 39-56.

Hull, D. L. 1970. Contemporary systematic philosophies. *Annual Review of Ecology and Systematics.* 1: 19-54.

Jacobson, G. G. 1907. [Die Käfer Russlands und Westeuropas. Ein Handbuch zum Bestimmen der Käfer] Part 5: p. 321-400. [Work is in Russian. Title cited above is from *Zoological Record* for 1907. I saw an unpublished English translation of the work.]

Jacquelin du Val, P. N. C. 1857. *Manuel entomologique. Genera des coléoptères d'Europe . . .*, vol. 1. Chez A. Deyrolle, Naturaliste, Paris. cclxxvi, 140 p. 56 pls.

Jeannel, R. 1938. Les migadopides (Coleoptera Adephaga), une lignée subantarctique. *Revue fr. Ent.* 5 (1): 1-55.

Jeannel, R. 1940. Les calosomes (Coleoptera Carabidae). *Mém. Mus. natn. Hist. nat.*, Paris 13 (1): 1-24, 8 pls.

Jeannel, R. 1942a. *Coléoptères carabiques, Deuxième partie. Faune de France* 40: 473-1173. [facsimile of book, Kraus Reprint Limited, Nendeln, Liechtenstein, 1967].

Jeannel, R. 1942b. La genèse des faunes terrestres, éléments de biogéographie. *Presses Universitaires de France*, Paris, viii, 513 p., 8 pls.

Jeannel, R. 1946. Sur la systématique des harpalides d'Afrique et Madagascar. *Revue fr. Ent.* 12 (4): 157-162.

Jeannel, R. 1948. *Coléoptères carabiques de la Region malgache (Deuxième partie). Faune. Emp. fr.* p. 373-765.

Jedlička, A. 1957. Neue Carabiden aus der Palaearktischen Region (Coleoptera). *Acta Entomologica Musei Nationalis.* 31 (473): 91-101.

Johnson, N. E. and R. S. Cameron. 1969. Phytophagous ground beetles. *Ann. ent. Soc. Am.* 62 (4): 909-914.

King, P. G. 1958. Evolution of modern surface features of western North America. p. 3-60. In C. L. Hubbs (ed.), *Zoogeography*, Publ. 51. American Association for the Advancement of Science, Washington, D. C.

Kitching, J. W., J. W. Collinson, D. H. Elliot, and E. H. Colbert. 1972. *Lystrosaurus* zone (Triassic) fauna from Antarctica. *Science.* 175: 524-527.

Kuschel, G. 1963. Problems concerning an Austral Region. p. 443-449. In J. L. Gressitt (ed.) *Pacific Basin Biogeography*. Bishop Museum Press, Honolulu.

Lacordaire, J. T. 1854. *Histoire naturelle des insectes. Genera des coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes*, tome premier contenant les familles des Cicindélètes, Carabiques, Dytiscides, Gyrinides et Palpicornes. Librairie Encyclopédique de Roret, Paris. xx, 486 p.

LaFerté-Senectere, F. T. 1841a. Notice sur un nouveau genre de carabique de la tribu des harpaliens. *Annls Soc. ent. Fr.* 10: 201-204.

LaFerté-Senectere, F. T. 1841b. Description de dix carabiques nouveaux du Texas et d'une espèce nouvelle de buprestide de France. *Revue Zoologique par la Société Cuvierienne.* 1841: 37-51.

Larson, D. J. 1969. A revision of the genera *Philophuga* Motschulsky and *Tecnophilus* Chaudoir with notes on the North American Callidina (Coleoptera: Carabidae). *Quaest. ent.* 5: 15-84.

LeConte, J. L. 1848. A descriptive catalogue of the geodrophagous Coleoptera inhabiting the United States east of the Rocky Mountains. *Ann. Lyc. natur. Hist. New York.* 4: 173-474. [Pages after "233" are numbered 100 pages too high due to printing error; for example,

the actual page "374" is numbered as "474".].

LeConte, J. L. 1853. Notes on the classification of the Carabidae of the United States. *Trans. Am. phil. Soc.* 10: 363-403.

LeConte, J. L. 1863. New species of North American Coleoptera prepared for the Smithsonian Institution, part I. *Smithson. misc. Collns* 167: 1-86.

Leng, C. W. 1915. List of the Carabidae of Florida. *Bull. Am. Mus. nat. Hist.* 34: 555-601.

Leopold, A. S. 1959. Wildlife of Mexico. The game birds and mammals. University of California Press, Berkeley and Los Angeles. 568 p.

Lindroth, C. H. 1957. The principal terms used for male and female genitalia in Coleoptera. *Opusc. ent.* 22 (2-3): 241-256.

Lindroth, C. H. 1968. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. part 5. *Opusc. ent. Suppl.* 33: 649-944.

Lindroth, C. H. 1969a. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, part 1. *Opusc. ent. Suppl.* 35: i-xlviii.

Lindroth, C. H. 1969b. In C. H. Lindroth and R. Freitag, North American ground-beetles (Coleoptera, Carabidae, excluding Cicindelinae) described by Thomas Say: designation of lectotypes and neotypes. *Psyche.* 76 (3): 326-361.

Lindroth, C. H. and E. Palmen. 1956. 16. Coleoptera. p. 69-75. In S. L. Tuxen (ed.). *Taxonomists' Glossary of Genitalia in Insects.* Copenhagen.

Lutshnik, V. 1921. Review of the Russian species of the genus *Anisodactylus* Dej. *Acta Instituti Agronomici Stauropolitani*, 1: 3-5. [I was unable to locate this work and, above title is from Zoological Record for 1921].

Lutshnik, V. 1922. De Harpalinis Novis Vel Parum Cognitis. *Acta Instituti Agronomici Stauropolitani*. 1: 51-65. [I was unable to locate this work, and above title is from Zoological Record for 1921. Jeannel (1942) cited subgenus *Pseudhexatrichus* as being described on page 3.].

MacGinitie, H. D. 1958. Climate since the Late Cretaceous. p. 61-79. In C. L. Hubbs (ed.), *Zoogeography.* American Association for the Advancement of Science, Publ. 51. Washington, D. C.

MacLeay, W. J. 1864. Descriptions of new genera and species of Coleoptera from Port Dension. *Transactions of the Entomological Society of New South Wales.* 1: 106-130.

MacLeay, W. S. 1825. Number I. of *Annulosa Javanica*, or an attempt to Illustrate the natural affinities and analogies of the insects collected in Java by Thomas Horsfield, M. D., F. L., & G. S. and deposited by him in the Museum of the Honourable East-India Company. Kingsbury, Parbury, and Allen, London. xii, 50 p.

Malfait, B. T. and M. G. Dinkelman. 1972. Circum-Caribbean tectonic igneous activity and the evolution of the Caribbean plate. *Bull. geol. Soc. Am.* 83: 251-271.

von Mannerheim, C. G. 1843. Bietrag zur Käferfauna der Aleutischen Inseln, der Insel Sitka und Neu-Californiens. *Moskovskoe Obschestvo Ispateleli Prirody.* 16 (2): 175-314.

Martin, P. S. 1958. Pleistocene ecology and biogeography of North America. p. 375-420. In C. L. Hubbs (ed.) *Zoogeography.* Publ. 51. American Association for the Advancement for Science, Washington, D. C.

Martin, P. S. and B. E. Harrell. 1957. The Pleistocene history of temperate biotas in Mexico and eastern United States. *Ecology* 38 (3): 468-480.

Martin, P. S. and P. J. Mehringer. 1965. Pleistocene pollen analysis and biogeography of the Southwest. p. 433-451. In H. E. Wright and D. G. Frey (ed.). *The Quaternary of the United States.* Princeton University Press, New Jersey.

Maslin, T. P. 1952. Morphological criteria of phyletic relationships. *Syst. Zool.* 1 (2): 49-70.

Matthew, W. D. 1915. Climate and evolution. *Ann. N. Y. Acad. Sci.* 24: 171-318.

Mayr, E. 1969. Principles of Systematic Zoology. McGraw-Hill, New York, 428 p.

Moore, I. 1937. A list of the beetles of San Diego County, California. Occ. Pap. S. Diego Soc. nat. Hist. 2: 1-109.

Moreau, R. E. 1966. The bird faunas of Africa and its islands. Academic Press, New York. viii, 424 p.

Morgan, W. J., P. R. Vogt and D. F. Falls. 1969. Magnetic anomalies and sea floor spreading on the Chile Rise. Nature, Lond. 222: 137-142.

Müller, G. 1938. Di alcuni Carabidi nuovi o poco noti dell' Africa orientale. Annali Mus. civ. Stor. nat. Giacomo Doria. 58: 222-254.

Murray, A. 1858. List of Coleoptera received from Old Calabar, on the west coast of Africa. Ann. Mag. nat. Hist. ser. 3, 2: 340-348.

Nelson, G. L. 1971a. "Cladism" as a philosophy of classification. Syst. Zool. 20 (3): 373-376.

Nelson, G. L. 1971b. Paraphyly and polyphyly: redefinitions. Syst. Zool. 20 (4): 471-472.

Newman, E. 1838. Entomological notes. The Entomological Magazine. 5: 168-182, 372-402. 483-500.

Noonan, G. R. 1968. A revision of the genus *Dicheirus* Mannerheim 1843 (Col. Carabidae). Opusc. ent. 33: 281-304. [Distributed by editor of Opuscula Entomologica as preprint on 5 July, 1968. Also appeared as article in journal on 15 November, 1968. For purposes of priority taxonomic changes date from distribution of preprint].

Notman, H. 1919. Records and new species of Carabidae. J. N. Y. ent. Soc. 28 (1): 225-237.

Peringuey, L. 1896. Descriptive catalogue of the Coleoptera of South Africa. Part I. Trans. S. Afr. phil. Soc. 7: xiv, 1-623, 10 pls.

Perty, J. A. M. 1830. Insecta brasiliensia. p. 1-60. In Delectus Animalium Articulatorum, Quae in Itinere Per Brasiliam Annis MDCCCVIII-MDCCXX Jussu et Auspiciis Maximiliani Josephi I. Bavariae Regis Augustissimi Peracto . . . fascicle 1.

Puel, L. 1931. Notes sur les carabiques. Troisième note. 4. Les *Anisodactylus* paléarctiques. Annls Soc. ent. Fr. 1931: 61-85.

Putzeys, J. A. A. H. 1878. Descriptions de carabides nouveaux de la Nouvelle Grenade rapportés par M. E. Steinheil. Mittheilungen des Münchener Entomologischen Vereins. 2: 54-76.

Raven, P. H. 1967. The floristics of the California Islands. p. 57-67. In R. N. Philbrick (ed.), Proceedings of the Symposium on the Biology of the California Islands. Santa Barbara Botanic Garden, Santa Barbara, California.

Redtenbacher, L. 1868. Coleopteren. p. iv, 1-249, tables 1-5. In L. Redtenbacher, H. de Saussure, J. Sichel, G. L. Mayr, and F. Brauer, Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1859 unter den Befehlen des Commodore B. von Wüllerstorff-Urbair. Zoologischer Theil, Zweiter Band 1. Abtheilung.

Ross, H. H. 1965. Pleistocene events and insects. p. 583-596. In H. E. Wright and D. G. Frey (ed.), The Quaternary of the United States. Princeton University Press, New Jersey.

Savage, J. M. 1967. Evolution of the insular herpetofauna. p. 219-227. In R. N. Philbrick (ed.), Proceedings of the Symposium on the Biology of the California Islands. Santa Barbara Botanic Garden, Santa Barbara, California.

Say, T. 1823. Descriptions of insects of the families of Carabici and Hydrocanthari of Latreille, inhabiting North America. Trans. Am. phil. Soc. ser. 2, 2: 1-109.

Say, T. 1834. Descriptions of new North American Insects, and observations on some already described. Trans. Am. phil. Soc. 4: 409-470.

Schaeffer, C. 1910. Additions to the Carabidae of North America with notes on species already known. Sci. Bull. Mus. Brooklyn Inst. Arts Sciences. 1: 391-405.

Schauberger, E. 1926. Beitrag zur Kenntnis der paläarktischen Harpalinen. Coleopt. Zbl.

1 (1): 24-51.

Schauberger, E. 1932. Zur Kenntnis der paläarktischen Harpalinen. (Neunter Beitrag.). *Koleopt. Rdsch.* 18: 49-64.

Schauberger, E. 1933. Zur Kenntnis der indo-orientalischen Harpalinen, Erster Beitrag. *Ent. Anz.* 13: 133-136.

Schauberger, E. 1934. Zur Kenntnis der indo-orientalischen Harpalinen, vierter Beitrag. *Ent. Anz.* 14: 69-72.

Schaum, H. 1860. Naturgeschichte der Insecten Deutschlands. Erste Abtheilung, Coleoptera, Erster Band, Erste Hälfte. Nicolaische Verlagsbuchhandlung, Berlin, 791 p.

Schaum, H. 1862. Catalogus Coleopterorum Europae. Editio secunda aucta et emendata. 136 p.

Sclater, P. L. 1858. On the general geographical distribution of the members of the class Aves. *Journal of the Proceedings of the Linnean Society of London.* 2: 130-145.

Selander, R. B. and P. Vaurie. 1962. A gazetter to accompany the "Insecta" volumes of the "Biologia Centrali-Americana". *Am. Mus. Novit.* No. 2099: 1-70.

Simpson, G. G. 1961. *Principles of Animal Taxonomy.* Columbia University Press, New York. viii, 247 p.

Simpson, G. G. 1962. *Evolution and geography, an essay on historical biogeography with special reference to mammals.* Third Edition. University of Oregon Press, Eugene. 64 p.

Sloane, T. G. 1898. On Carabidae from West Australia, sent by Mr. A. M. Lea (with descriptions of new genera and species, synoptic tables, & c.). *Proc. Linn. Soc. N. S. W.* 23: 444-520.

Smith, A. G. and A. Hallam. 1970. The fit of the southern continents. *Nature, Lond.* 225: 139-144.

Tanaka, K. 1958. Anisodactylini of Japan, with description of a new Formosan *Chydaeus* (Carabidae, Coleoptera). *Mushi,* 32 (8): 83-92.

Tanner, V. M. 1927. A preliminary study of the genitalia of female Coleoptera. *Trans. Am. ent. Soc.* 53: 5-50.

Torre-Bueno, J. R. 1962. A glossary of entomology, and supplement A. (ed. by G. S. Tulloch). Third printing. Brooklyn Entomological Society, Brooklyn. 336 p., 9 pls., 36 p. suppl.

Tschitscherine, T. 1897. Carabiques nouveaux ou peu connus. *L'Abeille. Mémoires d'Entomologie.* 29: 45-75.

Tschitscherine, T. 1898. Quelques remarques sur le genre *Anisodactylus* Dejean. *Bull. Soc. ent. Fr.* 1898: 138.

Tschitscherine, T. 1900. Mémoire sur la tribu des Harpalini. *Trudy russk. ent. Obshch.* 34: 335-370.

Tschitscherine, T. 1901. Genera des Harpalini des regions paléarctique et paléanarctique. *Trudy russk. ent. Obshch.* 35: 215-251.

United States Department of Agriculture. 1941. *Yearbook of Agriculture. Climate and Man.* United States Government Printing Office, Washington, D. C. 1248 p.

Wallace, A. R. 1876. *The geographical distribution of animals.* London, Macmillan, and Co., 2 vol. 503 + 607 p.

Westwood, J. O. 1838. Synopsis of the genera of British insects, p. 1-48. In J. O. Westwood, *Introduction to the modern classification of insects: founded on the natural habits and corresponding organisation of the different families.* Longman, Orme, Brown, Green, and Longmans, London.

Whitehead, D. R. 1965. Palynology and Pleistocene phytogeography of unglaciated eastern North America. p. 417-432. In H. E. Wright and D. G. Frey (ed.). *The Quaternary of the*

United States. Princeton University Press, New Jersey.

Whitehead, Donald Robert. [not the same person as D. R. Whitehead cited above]. 1972. Classification, phylogeny, and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaritini). *Quaest. ent.* 8 (3): 131-348.

Wiedemann, C. R. W. 1823. Zweihundert neue Käfer von Java, Bengalen und dem Borgebirge der gutten Hoffnung. *Zoologisches Magazin*. 2 (1): 1-164.

Wilson, E. W. 1961. The nature of the taxon cycle in the Melanesian ant fauna. *Am. Nat.* 95 (882): 169-193.

Wolfe, J. A. 1969. Neogene floristic and vegetational history of the Pacific Northwest. *Madrono* 20: 83-110.

Wolfe, J. A. and E. B. Leopold. 1967. Neogene and early Quaternary vegetation of northwestern North America and northeastern Asia. p. 193-206. *In* D. M. Hopkins (ed.). *The Bering Land Bridge*. Stanford University Press, Stanford, California.

Table 1. Color combinations of Panamanian morph of *Notiobia parilis*.

Locality	Color Combinations				
	I	II	III	IV	V
Barro Colorado, Panama	2 ♂♂, 8 ♀♀	2 ♂♂, 2 ♀♀	2 ♂♂		
Bugaba, Panama	1 ♂				
Archipelago de las Perlas, Panama	1 ♀				
La Caja, 8 Km W. San Jose, Costa Rica	1 ♂	1 ♂, 1 ♀	1 ♂		
San Jose, Costa Rica		3 ♂♂, 1 ♀		2 ♂♂, 1 ♀	
Turrialba, Costa Rica					1 ♂
Costa Rica			1 ♀		

I = head and pronotum predominantly green but with slight cupreous tinge, elytron purplish.

II = head and pronotum predominantly cupreous but with slight greenish tinge, elytron purplish.

III = head and pronotum predominantly aeneous but with slight cupreous and/or greenish tinge, elytron purplish.

IV = head and pronotum bluish green, elytron bluish purple.

V = head, pronotum, and elytron bluish green.

Table 2. Plesiomorphic and apomorphic character states used in Figs. 240, 241.

No.	Character	Character State	
		Plesiomorphic	Apomorphic
Color			
1	of body and dorsum	body rufopiceous to black, dorsum lacking metallic tinges	dorsum of many specimens with metallic tinges present (a) dorsum with metallic tinge always present (b) dorsum brightly bi-colored (c) dorsum brightly tri-colored (d) dorsum pale rufotestaceous except for median darker areas (e) entire body depigmented
Microsculpture			
2	of dorsum	not causing iridescence	causing iridescence
3	of pronotum	isodiametric mesh	very fine dense lines
4	of elytron	isodiametric mesh	obsolete except at apex
5	of elytron	granulate slightly transverse mesh not causing iridescence	extremely fine dense lines causing iridescence
Body Pubescence			
6		generally absent	venter and dorsum of head and pronotum and part or all of elytron pubescent (a) all of body pubescent
Head			
7	frontal fovea	not obsolete	obsolete and obscured by punctures
8	clypeo-ocular prolongation	absent	present in most species (a) present in all species
9	fronto-clypeal suture	unmodified	very deep and prominent, obliterating frontal fovea

Table 2. Plesiomorphic and apomorphic character states used in Figs. 240, 241. (continued).

No.	Character	Character State	
		Plesiomorphic	Apomorphic
10	eye	normal	large and bulging
11	gena	wide	narrow
12	antennal sulcus	absent	present
13	mandible	unmodified	apex striate dorsally (a) elongate and striate dorsally
14	1 seta at each side of mentum	present	absent
15	mental tooth	moderate tooth present	absent (a) moderate tooth present (b) very prominent tooth present
16	mentum and submentum	completely separate	free medially in all specimens but fused laterally in most spec- imens (a) completely fused
17	ligula apex	not to slightly expanded laterally	moderately to strongly expanded laterally. (a) not to slightly ex- panded laterally
18	setae on paraglossa	absent	present on dorsum and lateral margins (a) present in most spe- cies on dorsum and/or lateral margins
19	Pronotum shape	semi-rectangular, with side slightly to moder- ately curved towards posterior angle	orbiculate (a) cordate (b) cordate, with side strongly sinuate before posterior angle

Table 2. Plesiomorphic and apomorphic character states used in Figs. 240, 241. (continued).

No.	Character	Character State	
		Plesiomorphic	Apomorphic
20	posterior angle	slightly obtuse to slightly acute	strongly rounded (a) very acute and outward projected
21	lateral depression	lacking sharply delimited lateral depression	with sharply delimited lateral depression
22	apparent inflection of integument	absent	integument with apparent inflection at edge of lateral depression
23	apical bead	present at least laterally	absent
24	no. lateral seta each side	1	2
25	non-setigerous punctures	absent or very few	numerous, small dense punctures present
26	pubescence	absent	present along lateral part of apex (a) present along sides and lateral part of base and apex
Legs			
27	Forefemur of ♂	lacking tooth on inner margin	with tooth on inner margin in most ♂♂
28	Foretibia	unmodified	apical portion strongly expanded laterally and with large excavate dilation at external apex
29	Foretibia of ♂	inner proximal margin only very slightly emarginate	inner proximal margin moderately emarginate (a) inner proximal margin strongly emarginate
30	Foretibial apical spur	lanceolate	trifid

Table 2. Plesiomorphic and apomorphic character states used in Figs. 240, 241. (continued).

No.	Character	Character State	
		Plesiomorphic	Apomorphic
31	Hindtibial apical spur	lanceolate	spatulate
32	segments II to IV of hindtarsus of both sexes and segments II to IV of fore- and midtarsus of ♀	unmodified	with dense ventro-lateral cover of somewhat thickened setae
33	hindtarsus	not shortened, first segment 3 or more times long as wide	shortened, first segment 2 or less times long as wide in most specimens
34	Elytron scutellar stria	unmodified	absent or vestigial
35	dorsal non-setigerous punctures	absent	row present on odd and in some specimens also even intervals (a) all intervals with small, dense punctures
36	dorsal setigerous punctures on intervals	1, rarely 2, on III	3 to many on III (a) row of punctures extended towards base on III (b) row of punctures on III, V, VII
37	stria	evenly rounded, not deep and prominent	semi-rectangular in form, deep and prominent
38	Abdomen extra setae on sterna	absent	present in some (a) present in all specimens of both sexes
39	no. ambulatory setae on sternum VI of ♀	4	2

Table 2. Plesiomorphic and apomorphic character states used in Figs. 240, 241. (continued).

No.	Character	Character State	
		Plesiomorphic	Apomorphic
40	apex sternum VI of ♀	unmodified	with slight semi-plate like swelling medially (a) with prominent plate like swelling medially
41	Male genitalia median lobe	symmetric	asymmetric
42	apical disc of median lobe	absent	very slight disc (a) small disc (b) moderate sized disc (c) "button" shaped disc
43	Female genitalia valvifer	moderately sclerotized, not vestigial, lateral margin discrete	lateral margin semimembranous and not discrete (a) vestigial
44	valvifer	triangular in form and with distal setae	subtriangular in form and with distal setae (a) subtriangular in form and lacking distal setae (b) subtriangular in form, lacking distal setae, with concave area at distal margin
45	valvifer	triangular in form and not lobed	lobed
46	segments of stylus	separate	fused
47	setae on basal segment of stylus	absent	1 or 2 small setae on distal lateral margin in many specimens (a) 1 or 2 small indistinct setae on distal lateral margin (b) 1 or 2 (rarely 3) short setae on distal lateral margin (c) 2 or more prominent long setae on distal lateral

Table 2. Plesiomorphic and apomorphic character states used in Figs. 240, 241. (concluded).

No.	Character	Character State	
		Plesiomorphic	Apomorphic
47			margin (d) setae on distal lateral and mesal mar- gins
48	extra setae on apical segment of stylus	absent	present
49	apical seg- ment of stylus	unmodified	elongate in most spec- imens
50	stylus	unmodified	moderately dilated lat- erally, lateral margin of apical segment finely serrate and with very small spines arising from between indentations (a) strongly dilated later- ally, lateral margin of ap- ical segment serrate and with short stout spines arising between serrations
51	proctiger	unmodified	modified into discrete sclerite (a) modified into paddle shaped sclerite free distal- ly from tergum (b) absent
52	Habitat climate of habitat	generally temperate	generally tropical

Table 3. Convergent character states among genera and subgenera of the subtribe Anisodactylina.

Character state	Taxa
clypeo-ocular prolongation present	<i>Criniventer</i> ; 1 sp. of <i>Crasodactylus</i> ; <i>Cenogmus</i> ; some spp. of <i>Hypharpax</i> ; some specimens of species of <i>Scybalicus</i> ; common ancestor of <i>Notiobia</i> and <i>Diatypus</i> ; ancestor of Anisodactyloids.
eye large and protruding	some species of <i>Anisotarsus</i> ; common ancestor of <i>Notiobia</i> and <i>Diatypus</i> ; <i>Phanagnathus</i> ; <i>Pseudaplocentrus</i>
narrow gena	some species of <i>Anisotarsus</i> ; common ancestor of <i>Notiobia</i> and <i>Diatypus</i> ; <i>Phanagnathus</i> ; <i>Pseudaplocentrus</i>
mentum and submentum completely fused	<i>Anisostichus</i> ; Anisodactyloids except <i>Progonochaetus</i>
ligula apex expanded laterally	some specimens of <i>Notiobia</i> (<i>Anisotarsus</i>) <i>tucumana</i> ; "Paradiatypus" species group of <i>Diatypus</i> ; <i>Criniventer</i> ; <i>Rhysopus</i> ; ancestor of all temperate adapted Anisodactyloids (except for <i>Xestonotus</i>)
2 pronotal lateral setae on each side	<i>Progonochaetus</i> ; <i>Diachromus</i>
trifid foretibial apical spur	3 species of subgenus <i>Anisodactylus</i> ; <i>Rhysopus</i> ; <i>Hexatrichus</i> ; common ancestor of <i>Pseudodichirus</i> and <i>Gynandrotarsus</i> ; either in an ancestor of <i>Dicheirus</i> and <i>Gynandromorphus</i> or independently in each genus
short hindtarsus	<i>Cenogmus</i> ; <i>Hypharpax</i> ; <i>Geopinus</i> ; <i>Anadaptus</i>
3 or more dorsal setigerous punctures on elytral interval III	<i>Gnathaphanus</i> ; <i>Diatypus</i> ; <i>Anisostichus</i> ; many species of <i>Pseudognathaphanus</i>
extra setae on abdominal sterna	common ancestor of <i>Triplasarus</i> , <i>Crasodactylus</i> , <i>Cenogmus</i> , and <i>Hypharpax</i> ; common ancestor of <i>Criniventer</i> and <i>Pseudanisotarsus</i> ; ancestor of <i>tucumana</i> lineage within <i>Anisotarsus</i> ; <i>Hexatrichus</i> ; some species of subgenus <i>Anisodactylus</i> ; some species of <i>Anadaptus</i> ; <i>Spongopus</i>
apical segment of stylus elongate	<i>Progonochaetus</i> ; <i>Geopinus</i>

Table 4. Plesiomorphic and apomorphic character states used in Fig. 242.

No.	Character	Character State	
		Plesiomorphic	Apomorphic
Microsculpture			
1	of elytron	isodiametric mesh	obsolete medially in ♂
Head			
2	eye	normal	reduced in most specimens
3	gena	wide	narrow
4	mental tooth	present and of moderate size	absent or vestigial
5	ligula apex	narrow	moderately to strongly expanded laterally in most specimens
Pronotum			
6	posterior angle	slightly acute to slightly obtuse	moderately to strongly rounded
7	side	slightly to moderately curved towards posterior angle	rectilinear or sinuate before posterior angle
8	lateral bead	normal	very prominent
Legs			
9	no. setae on posterior margin of hind-femur	2 to 6	10 to 12
Elytron			
10	distal setae on intervals III, V, VII	absent	present
Hind wing			
11	state	full	vestigial or dimorphic
Abdomen			
12	extra setae on sterna IV and V	absent	present

Table 4. Plesiomorphic and apomorphic character states used in Fig. 242 (concluded).

No.	Character	Character State	
		Plesiomorphic	Apomorphic
13	no. setae on sternum VI of ♂	2	4
14	Male genitalia median lobe	symmetrical	asymmetrical
15	large spine on internal sac	present	absent

Table 5. Plesiomorphic and apomorphic character states used in Fig. 243.

No.	Character	Character State	
		Plesiomorphic	Apomorphic
1	Color green tinge on dorsum	absent	present in most specimens
2	Microsculpture of frons	isodiametric mesh	small punctures
3	Head clypeo-ocular prolongation	present	absent
4	raised transverse ridge behind clypeal apex	present	absent
5	Pronotum shape	at most slightly widened basally	moderately widened basally (a) prominently widened basally
6	posterior angle	slightly obtuse to slightly acute	broadly rounded
7	lateral bead	complete and moderately prominent	obsolete anteriorly (a) very prominent and thick
8	Legs first segment of protarsus of ♀	not expanded laterally	slightly to moderately expanded laterally (a) strongly expanded laterally
9	Elytron humeral tooth	absent	present
10	subapical sinuation	obsolete	moderately prominent
11	Abdomen no. of ambulatory setae on sternum VI of ♂	4	2 (4 in occasional specimens of <i>haplomus</i>)

Table 5. Plesiomorphic and apomorphic character states used in Fig. 243. (concluded).

No.	Character	Character State	
		Plesiomorphic	Apomorphic
Male Genitalia			
12	apical disc on median lobe	present	absent
13	arrangement of inverted internal sac inside median lobe	following shape of median lobe	irregularly coiled

Table 6. Distribution by numbers of species of the groups of Anisodactylina in the major faunal regions. (introduced species recorded only by their place of origin).

Taxa	Nearctic	Neotropical	Palearctic	Ethiopian	Oriental	Australian	Nearctic + Neotropical	Palearctic + Oriental	Oriental + Australian	Oriental + Palearctic + Ethiopian
<i>Allocinopus</i>						5				
<i>Triplosarus</i>						2				
<i>Crasodactylus</i>				1						1
<i>Cenogmus</i>						3				
<i>Hypharpax</i>				1	27					2
<i>Gnathaphanus</i> (1 in Polynesia)				5	17					2
<i>Pseudanisotarsus</i>	1									
<i>Criniventer</i>		1								
<i>Anisotarsus</i>	11	12				30	2			
<i>Notiobia</i>		27								
<i>Diatypus</i>				10						
<i>Anisostichus</i>		4								
<i>Scybalicus</i>			3							
<i>Progonochaetus</i>				37	1					
<i>Eudichirus</i>				3						
<i>Phanagnathus</i>				1						
<i>Pseudognathaphanus</i>			2	6						
<i>Chydaeus</i>		5			14	1		2		
<i>Harpalomimetes</i>					1				1	

Table 6. Distribution by numbers of species of the groups of Anisodactylina in the major faunal regions. (introduced species recorded only by their place of origin). (continued).

Taxa	Nearctic	Neotropical	Paleartic	Ethiopian	Oriental	Australian	Nearctic + Neotropical	Paleartic + Oriental	Oriental + Australian	Oriental + Paleartic + Ethiopian
<i>Rhysopus</i>					1					
<i>Xestonotus</i>	1									
<i>Anisodactylus</i>	12		11		1					
<i>Pseudanisodactylus</i>				2						
<i>Pseudhexatrichus</i>			2							
<i>Hexatrichus</i>			3							
<i>Pseudodichirus</i>			1							
<i>Gynandrotarsus</i>	10									
<i>Anadaptus</i>	8									
<i>Spongopus</i>	1									
<i>Aplocentrus</i>	2									
<i>Pseudaplocentrus</i>	1									
<i>Geopinus</i>	1									
<i>Pseudamphasia</i>	1									
<i>Amphasia</i>	1									
<i>Gynandromorphus</i>		1								
<i>Diachromus</i>			1							
<i>Dicheirus</i>		5								
Total endemic species	54	45	29	53	31	85				1

Table 6. Distribution by number of species of the groups of Anisodactylina in the major faunal regions. (introduced species recorded only by their place of origin). (concluded).

Taxa	Nearctic	Neotropical	Palearctic	Ethiopian	Oriental	Australian	Nearctic + Neotropical	Palearctic + Oriental	Oriental + Australian	Oriental + Palearctic + Ethiopian
Total number supra-specific taxa	12	5	9	7	9	7				1
Average number of endemic species per supra-specific taxon	4.5	9	3.6	7.6	3.4	12.1				1
Number of endemic supra-specific taxa	10	4	6	3	1	3				
% endemic supra-specific taxa	83	80	67	43	11	43				
Total no. spp. (includes non endemics)	56	47	32	54	39	89				
Total no. spp./taxon	4.7	9.4	3.5	7.7	4.3	12.7				

Table 7. Distribution of the genera and subgenera of the subtribe Anisodactylin in temperate and tropical regions.

Taxa	Temperate	Tropical
<i>Allocinopus</i>	x	
<i>Triplosarus</i>	x	
<i>Crasodactylus</i>	x	x
<i>Cenogmus</i>	x	
<i>Hyppharpax</i>	x	x
<i>Gnathaphanus</i>	x	
<i>Pseudanisotarsus</i>	x	
<i>Criniventer</i>	x	
<i>Anisotarsus</i>	x	
<i>Notiobia</i>		x
<i>Diatypus</i>		x
<i>Anisostichus</i>	x	
<i>Scybalicus</i>	x	
<i>Progonochaetus</i>		x
<i>Eudichirus</i>		x
<i>Phanagnathus</i>		x
<i>Pseudognathaphanus</i>		x
<i>Chydaeus</i>	x	
<i>Harpalomimetes</i>	x	x
<i>Rhysopus</i>		x
<i>Xestonotus</i>	x	
<i>Anisodactylus</i>	x	x (1 or 2 species only)

Table 7. Distribution of the genera and subgenera of the subtribe Anisodactylina in temperate and tropical regions. (concluded).

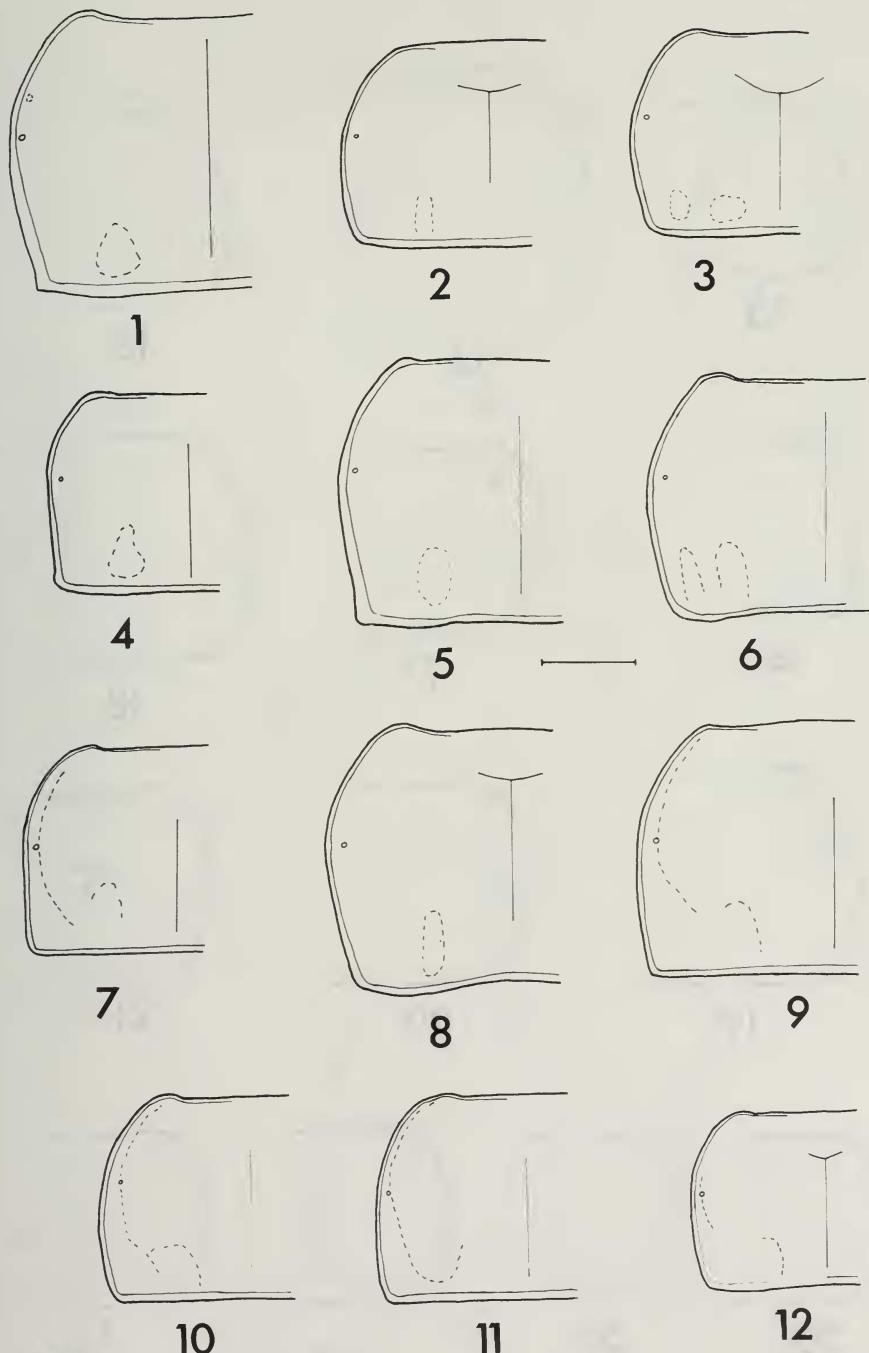
Taxa	Temperate	Tropical
<i>Pseudanisodactylus</i>	x	
<i>Pseudhexatrichus</i>	x	
<i>Hexatrichus</i>	x	
<i>Pseudodichirus</i>	x	
<i>Gynandrotarsus</i>	x	
<i>Anadaptus</i>	x	
<i>Spongopus</i>	x	
<i>Aplocentrus</i>	x	
<i>Pseudaplocentrus</i>	x	
<i>Geopinus</i>	x	
<i>Pseudamphasia</i>	x	
<i>Amphasia</i>	x	
<i>Gynandromorphus</i>	x	
<i>Diachromus</i>	x	
<i>Dicheirus</i>	x	
TOTAL	30	11
ENDEMICS	26	7

Table 8. Range extents of species of *Anisotarsus*.

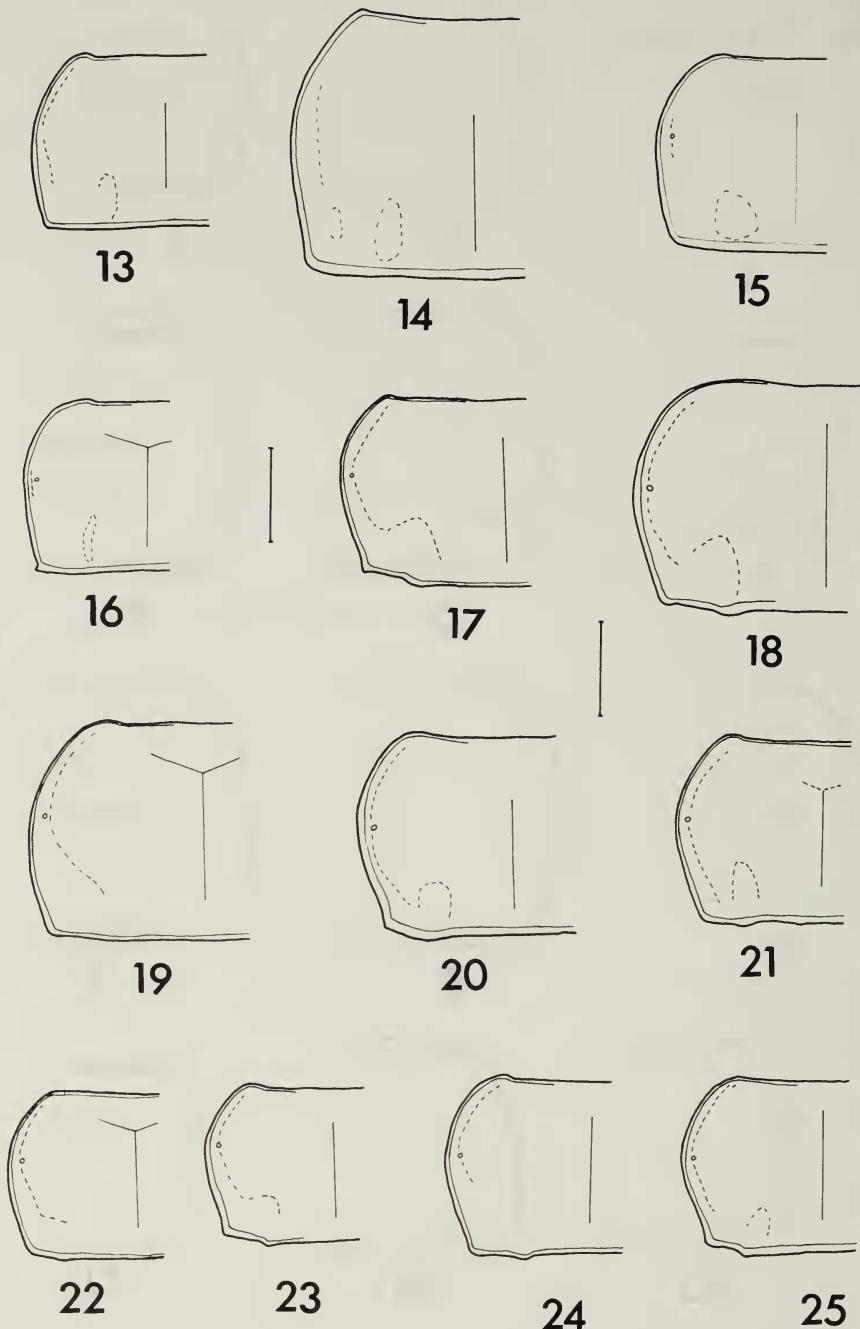
SPECIES Distance Range (in miles)	MAXIMUM RANGE EXTENT (in miles)
0-500	
<i>hilariola</i>	under 100
<i>lamprota</i>	150
<i>schlingeri</i>	375
<i>cyanippa</i>	425
501-1000	
<i>maculicornis</i>	725
<i>virescens</i>	750
<i>flebilis</i>	900
1001-2000	
<i>brevicollis</i>	1500
<i>purpurascens</i>	1650
<i>picea</i>	1750
<i>nitidipennis</i>	1850
2001-2950	
<i>mexicana</i>	2350
<i>terminata</i>	2950

Table 9. Range extents of species of *Gynandrotarsus*.

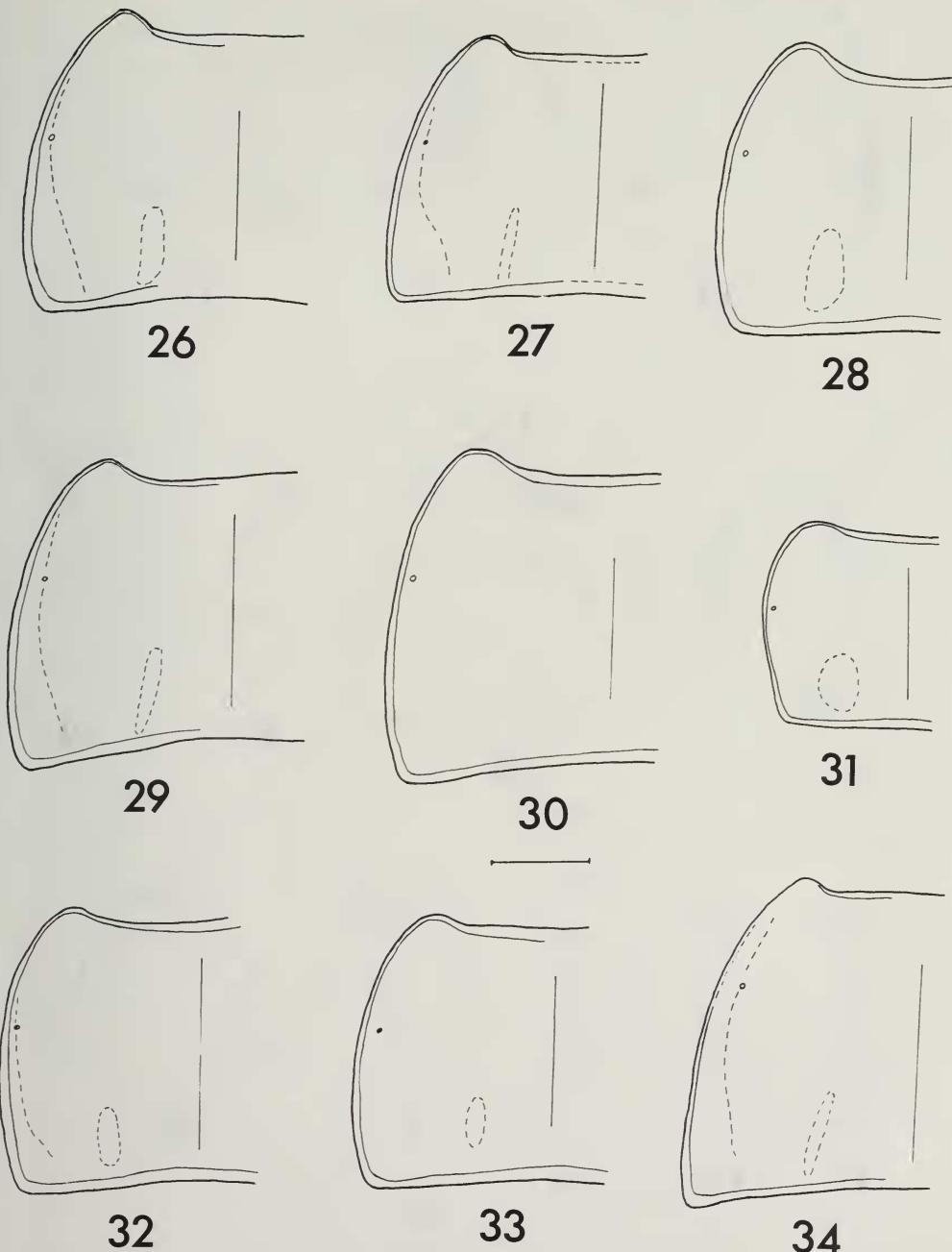
SPECIES Distance Range (in miles)	MAXIMUM RANGE EXTENT (in miles)
0-500	
none	
501-1000	
<i>harpaloides</i>	650
<i>darlingtoni</i>	850
<i>opaculus</i>	1000
1001-1500	
<i>texanus</i>	1250
<i>haplomus</i>	1400
<i>ovularis</i>	1500
<i>dulcicollis</i>	1500
1501-2000	
<i>anthracinus</i>	1650
<i>merula</i>	1900
2001-2250	
<i>rusticus</i>	2250



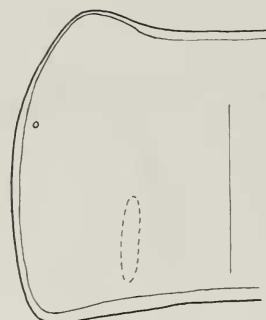
Figs. 1-12. Pronota of species of the subgenus *Anisotarsus*. 1. *lamprota*. 2. *virescens*. 3. *purpurascens*. 4. *schlingeri*. 5. *mexicana*. 6. *cyanippa*. 7. *picea*. 8. *hilariola*. 9. *maculicornis*. 10. *terminata* (Chicago, Illinois). 11. *terminata* (Texas). 12. *terminata* (Florida). (scale lines 1 mm.)



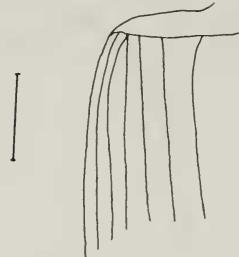
Figs. 13-16. Pronota of species of the subgenus *Anisotarsus*. 13. *terminata* (Mexico). 14. *brevicollis*. 15. *flebilis*. 16. *niti-dipennis*. Figs. 17-25. Pronota of species of the subgenus *Notiobia*. 17. *limbipennis*. 18. *leiroides*. 19. *cooperi*. 20. *melaena*. 21. *pallipes*. 22. *ewarti*. 23. *umbrifera*. 24. *obscura*. 25. *umbrata*. (scale lines 1 mm).



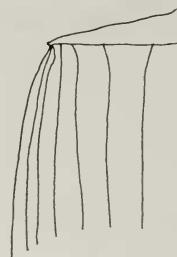
Figs. 26-34. Pronota of species of the subgenus *Gynandrotarsus*. 26. *oyularis*. 27. *rusticus*. 28. *dulcicollis*. 29. *merula*. 30. *anthracinus*. 31. *harpaloides*. 32. *texanus*. 33. *opaculus*. 34. *haplomus*. (scale line 1 mm).



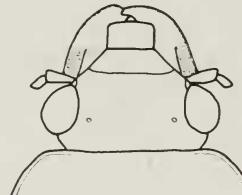
35



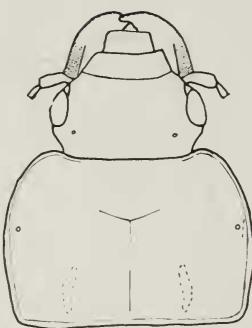
36



37



38



39



40



41



42



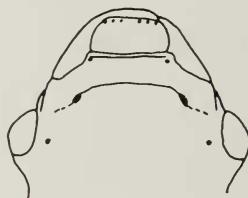
43



44

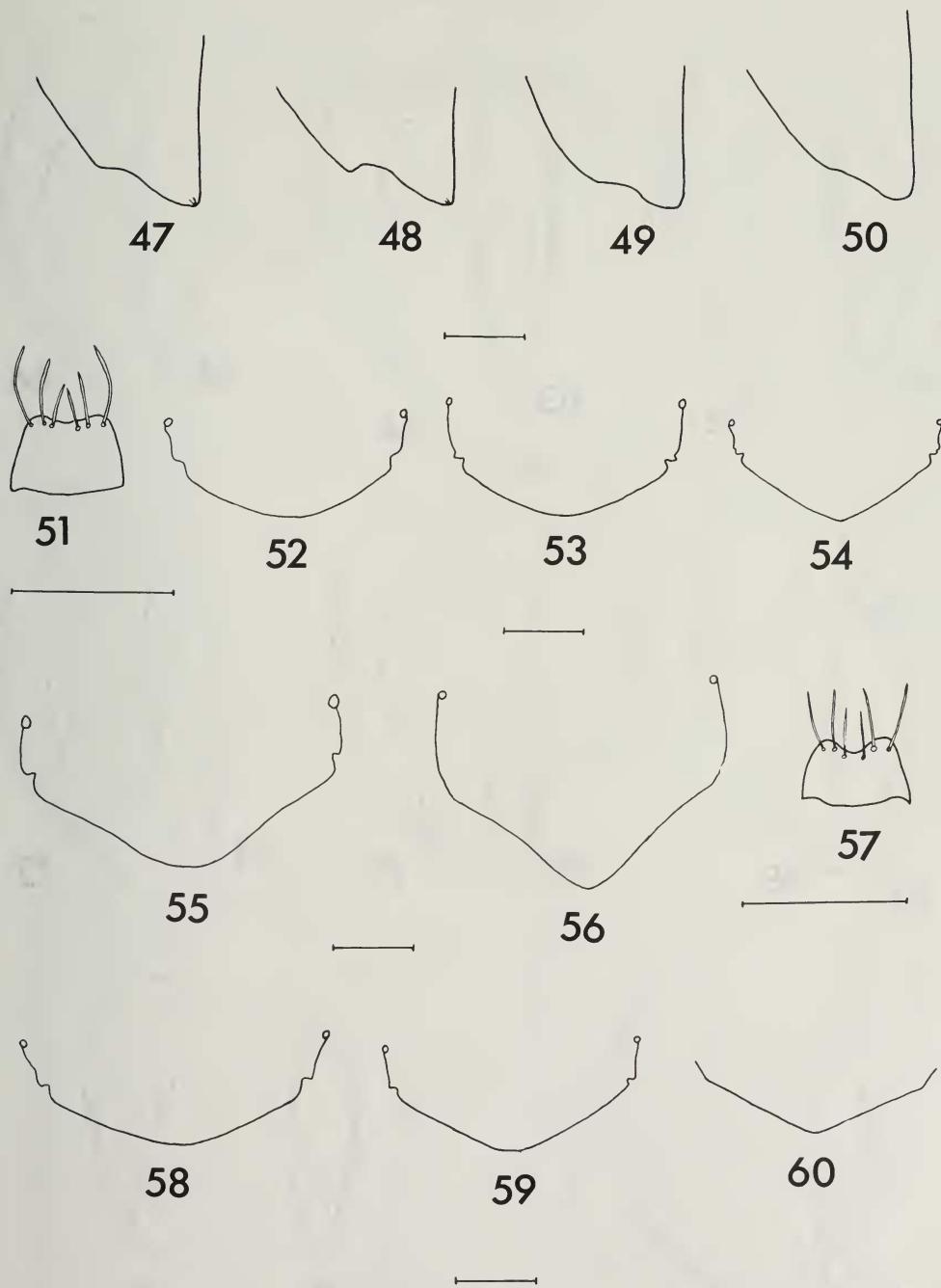


45

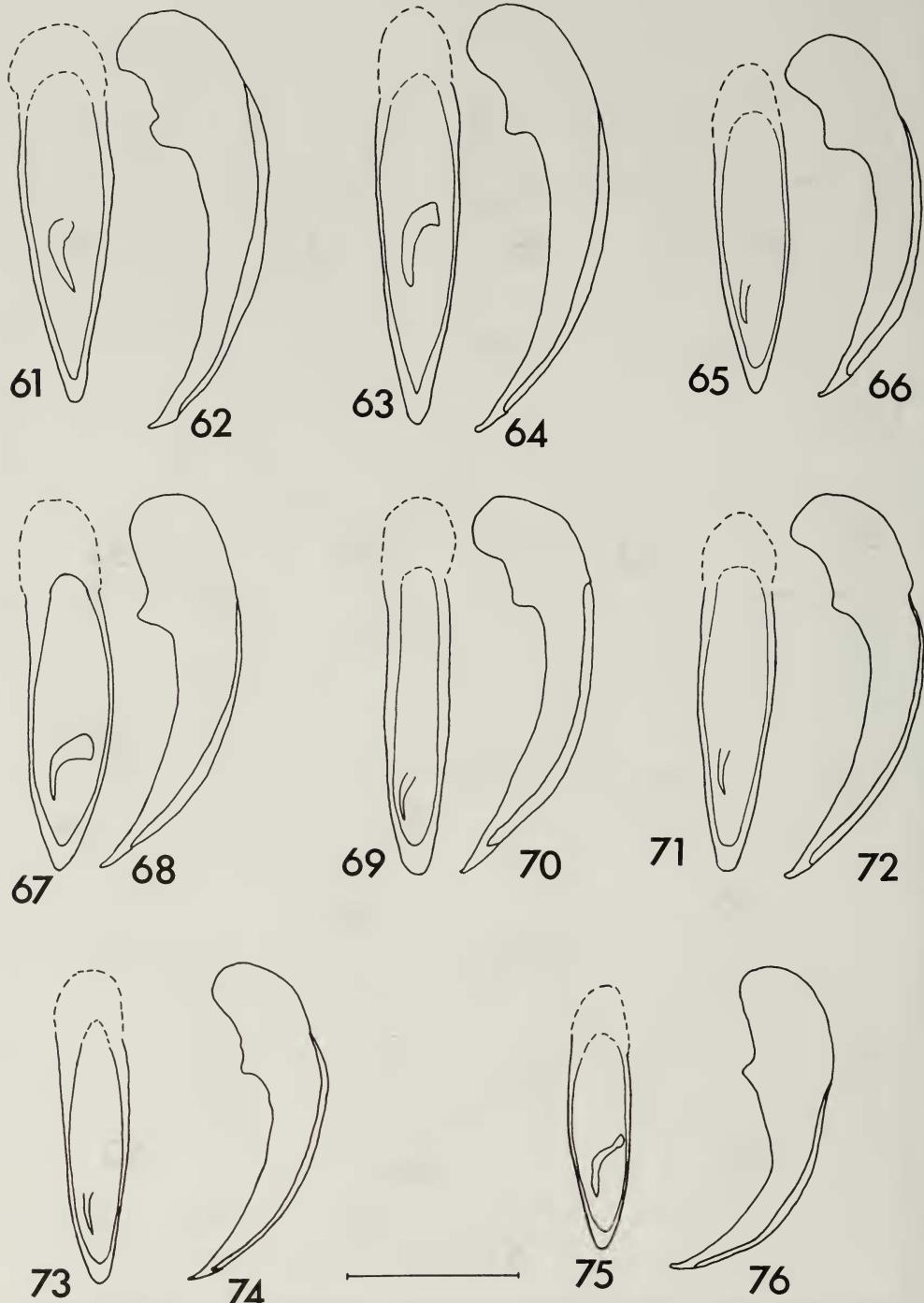


46

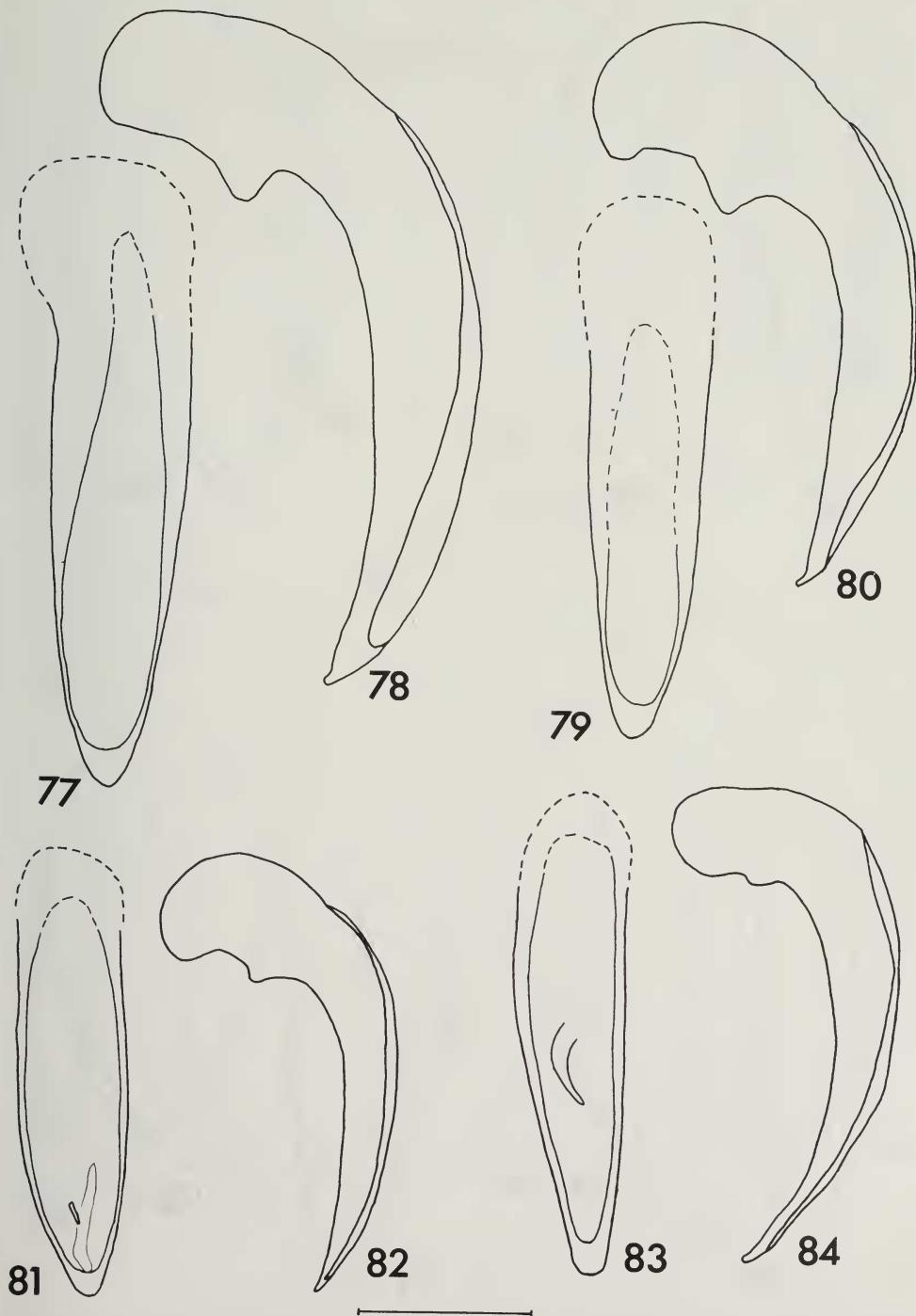
Figs. 35-37. Body parts of species of the subgenus *Gynandrotarsus*. 35. Pronotum of *darlingtoni*. 36. Humerus of *darlingtoni*. 37. Humerus of *anthracinus*. Figs. 38-39. Body parts of species of the subgenus *Anisotarsus*. 38. Head of *terminata*. 39. Head and pronotum of *nitidipennis*. Figs. 40-44. Venter of foretarsi of females of species of the subgenus *Gynandrotarsus* (setae and spines omitted). 40. *rusticus*. 41. *dulcicollis*. 42. *texanus*. 43. *opaculus*. 44. *harpaloides*. Figs. 45-46. Body parts of species of subgenus *Gynandrotarsus*. 45. Protibia and apical spur of *dulcicollis*. 46. Head of *opaculus* with clypeo-ocular prolongations indicated as dashed lines. (scale lines 1 mm).



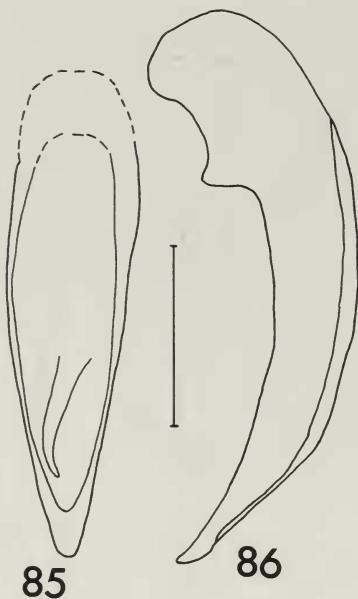
Figs. 47-50. Elytral apices of species of the subgenus *Notiobia*. 47. *limbipennis* (Mexico). 48. *limbipennis* (Panama). 49. *umbrata*. 50. *obscura*. Fig. 51. Labrum of *Notiobia* (*N.*) *obscura*. Figs. 52-56. Apex of abdominal tergum VIII of females of the subgenus *Notiobia*. 52. *pallipes*. 53. *umbrata*. 54. *umbrifera*. 55. *leiroides*. 56. *limbipennis*. Fig. 57. Labrum of *Notiobia* (*N.*) *ewarti*. Figs. 58-59. Apex of abdominal tergum VIII of females of the subgenus *Notiobia*. 58. *cooperi*. 59. *melaena*. Fig. 60. Apex of abdominal tergum VIII of female of *Anisodactylus* (*Gynandrotarsus*) *dulcicollis*. (scale lines 1 mm).



Figs. 61-76. Median lobes of male genitalia of species of the subgenus *Anisotarsus*. 61 & 62. Dorsal and lateral aspect of northern morph of *terminata*. 63 & 64. Dorsal and lateral aspect of *terminata* (Mexico, Nuevo Leon, 20.3 mi. N. Sabinas Hidalgo). 65 & 66. Dorsal and lateral aspect of *terminata* (Mexico, Hidalgo, 7.2 mi. S. Zimapán). 67 & 68. Dorsal and lateral aspect of *purpurascens*. 69 & 70. Dorsal and lateral aspect of *virescens*. 71 & 72. Dorsal and lateral aspect of *flebilis*. 73 & 74. Dorsal and lateral aspect of *nitidipennis*. 75 & 76. Dorsal and lateral aspect of *schlingeri*. (scale line 1 mm).

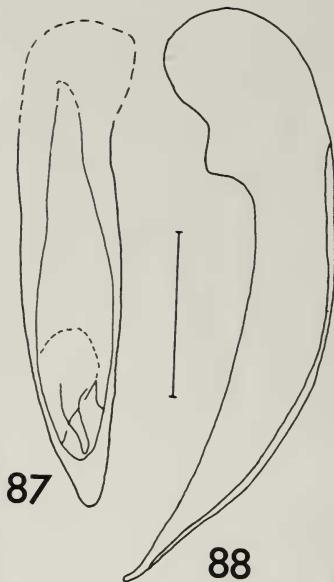


Figs. 77-84. Median lobes of male genitalia of species of the subgenus *Anisotarsus*. 77 & 78. Dorsal and lateral aspect of *lamprota*. 79 & 80. Dorsal and lateral aspect of *mexicana*. 81 & 82. Dorsal and lateral aspect of *picea*. 83 & 84. Dorsal and lateral aspect of *maculicornis*. (scale line 1 mm).



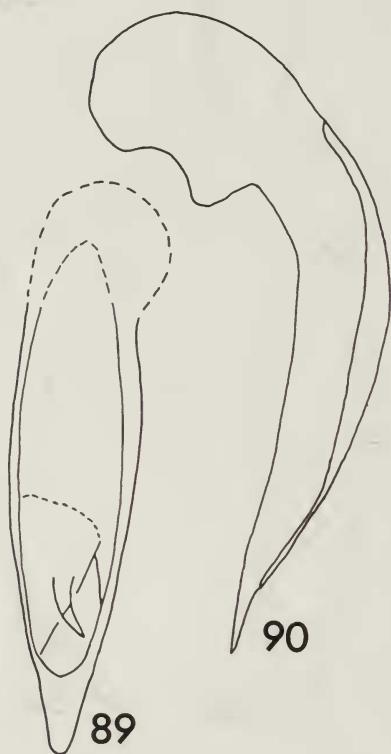
85

86



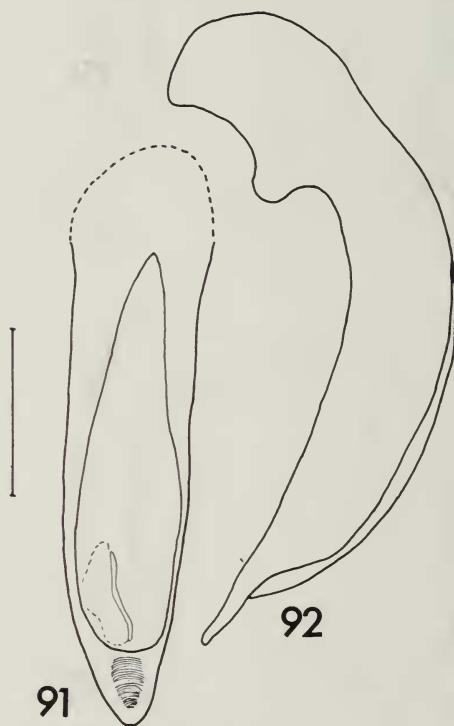
87

88



89

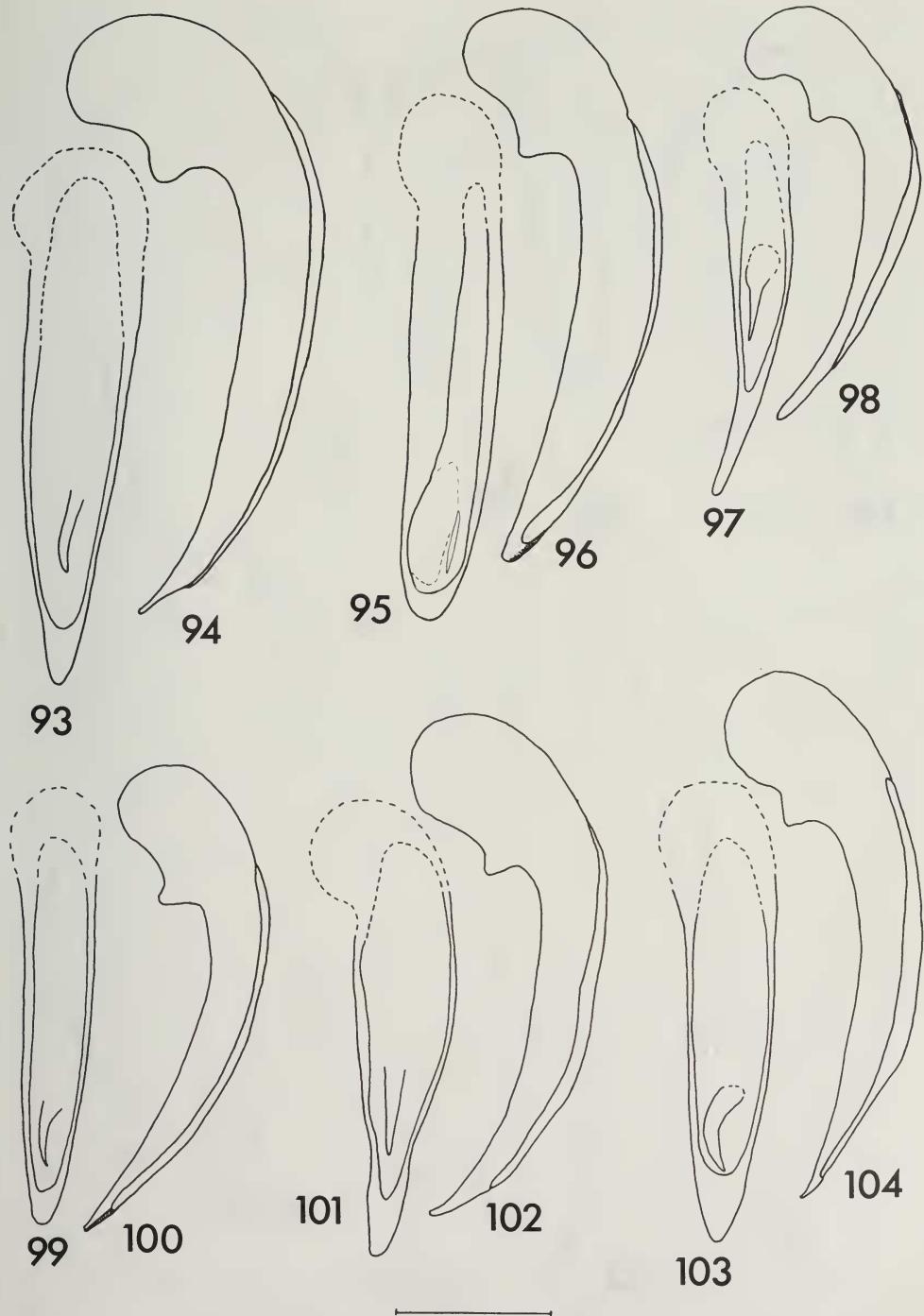
90



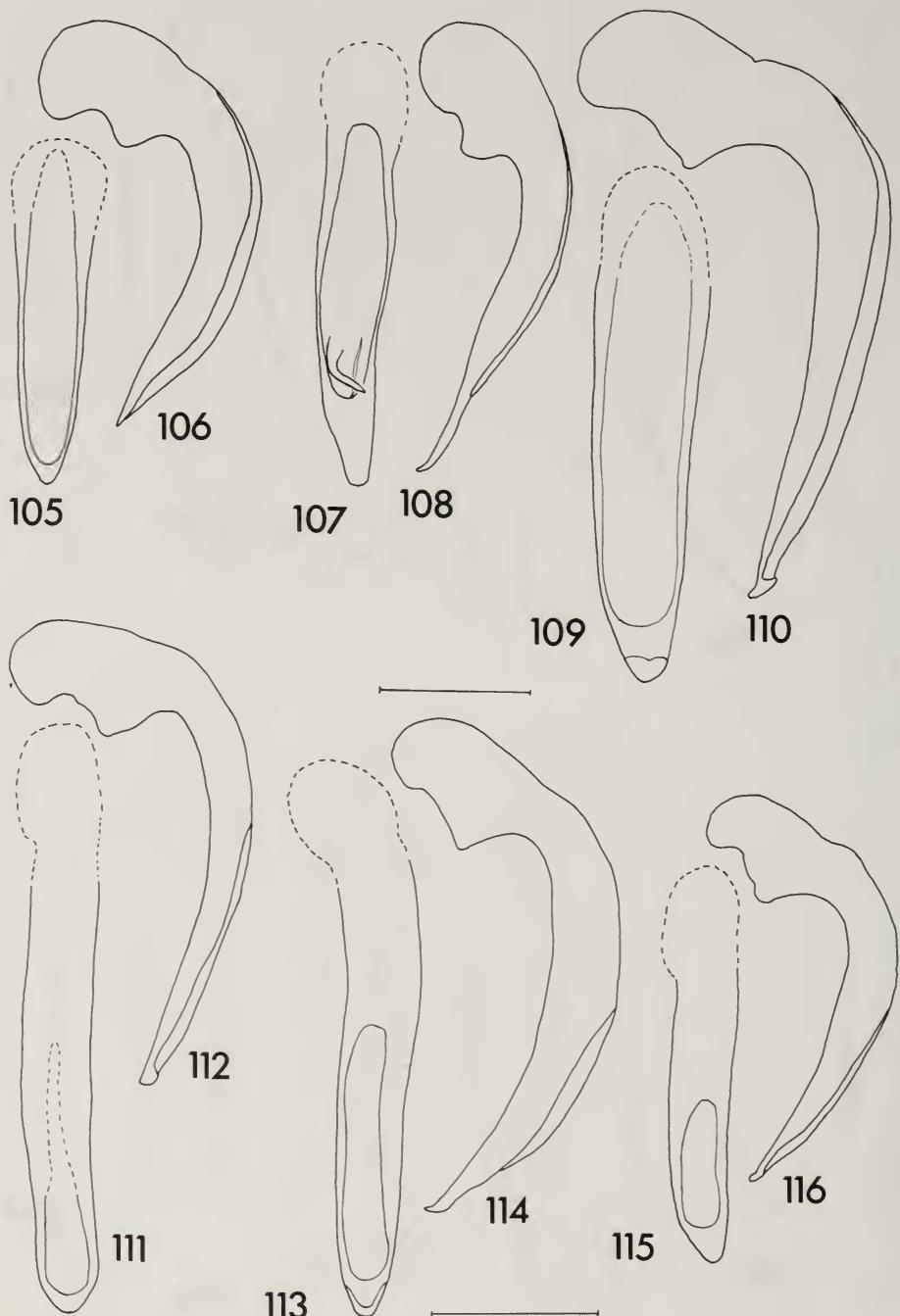
91

92

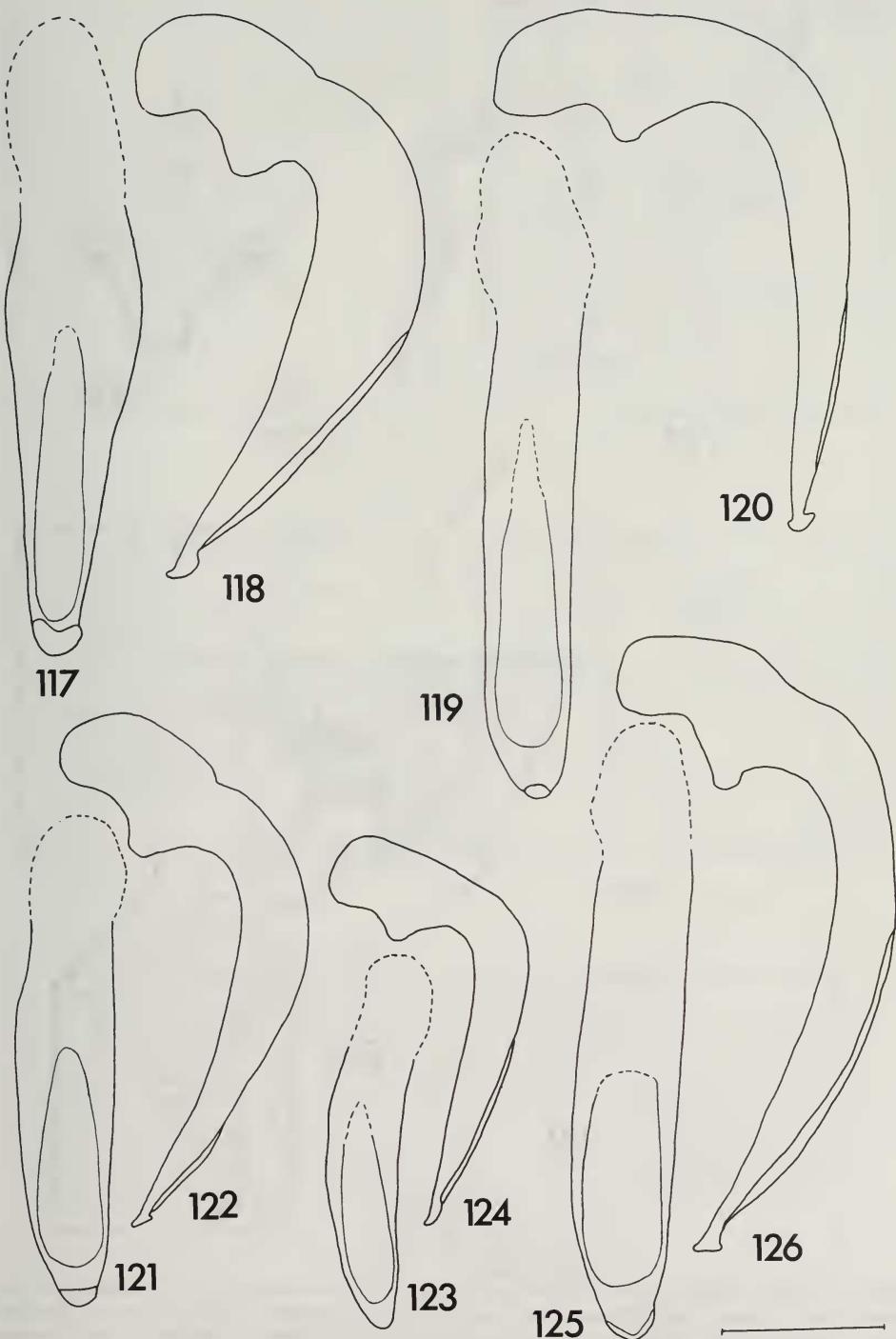
Figs. 85-90. Median lobes of male genitalia of species of the subgenus *Anisotarsus*. 85 & 86. Dorsal and lateral aspect of *brevicollis*. 87 & 88. Dorsal and lateral aspect of *cyanippa*. 89 & 90. Dorsal and lateral aspect of *hilariola*. Figs. 91 & 92. Dorsal and lateral aspect of median lobe of male genitalia of *Notiobia (N.) leiroides*. (scale lines 1 mm).



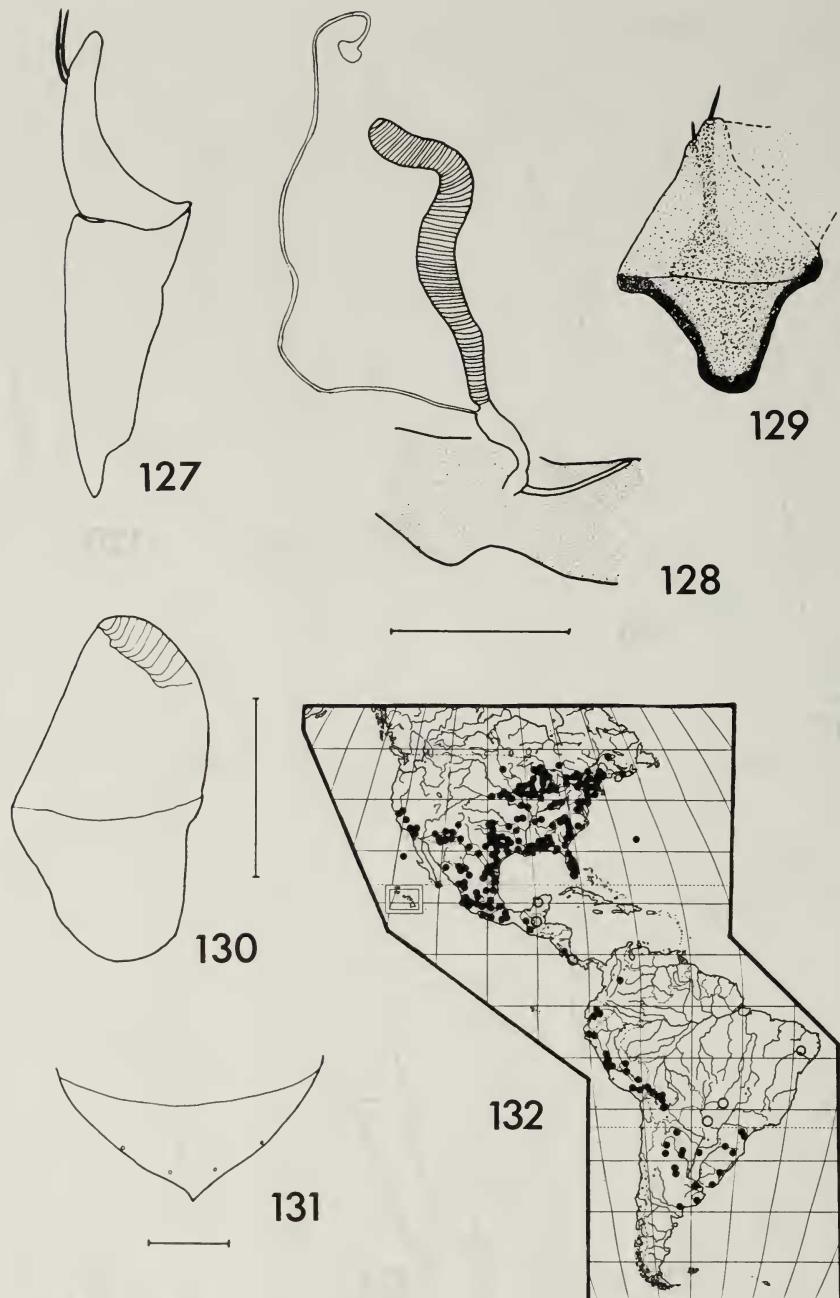
Figs. 93-104. Median lobes of male genitalia of species of the subgenus *Notioobia*. 93 & 94. Dorsal and lateral aspect of *melaena*. 95 & 96. Dorsal and lateral aspect of *limbipennis*. 97 & 98. Dorsal and lateral aspect of *umbrifera*. 99 & 100. Dorsal and lateral aspect of *obscura*. 101 & 102. Dorsal and lateral aspect of *pallipes*. 103 & 104. Dorsal and lateral aspect of *cooperi*. (scale line 1 mm).



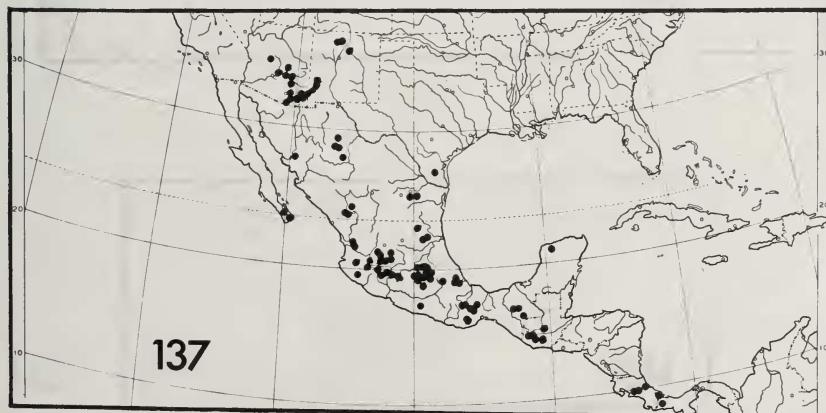
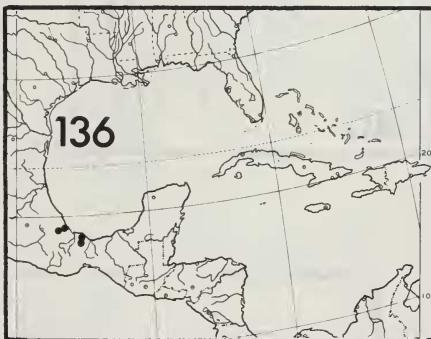
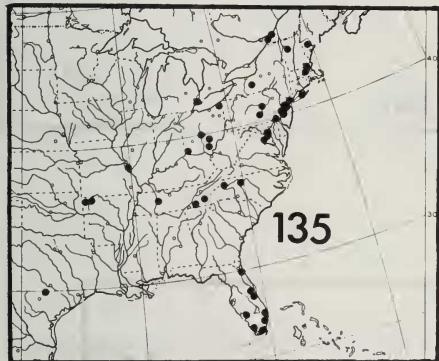
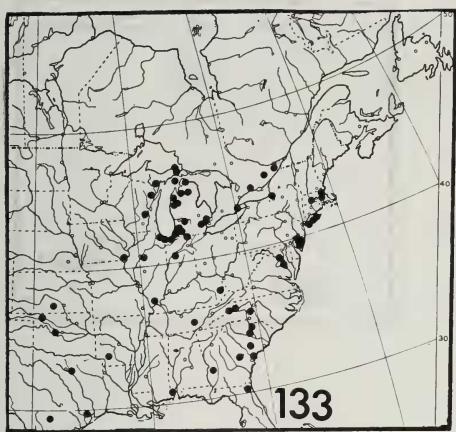
Figs. 105-108. Median lobes of male genitalia of species of the subgenus *Notiobia*. 105 & 106. Dorsal and lateral aspect of *umbrata*. 107 & 108. Dorsal and lateral aspect of *ewarti*. Figs. 109-116. Median lobes of male genitalia of species of the subgenus *Gynandrotarsus*. 109 & 110. Dorsal and lateral aspect of *darlingtoni*. 111 & 112. Dorsal and lateral aspect of *opaculus*. 113 & 114. Dorsal and lateral aspect of *haplomus*. 115 & 116. Dorsal and lateral aspect of *rusticus*. (scale lines 1 mm).



Figs. 117-126. Median lobes of male genitalia of species of the subgenus *Gynandrotarsus*. 117 & 118. Dorsal and lateral aspect of *dulcicollis*. 119 & 120. Dorsal and lateral aspect of *texanus*. 121 & 122. Dorsal and lateral aspect of *merula*. 123 & 124. Dorsal and lateral aspect of *harpaloides*. 125 & 126. Dorsal and lateral aspect of *ovularis*. (scale line 1 mm).



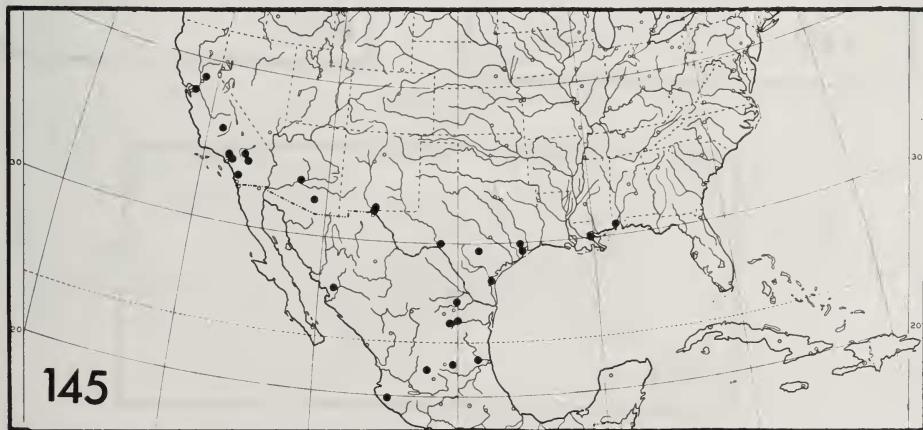
Figs. 127-129. Female genitalia of species of the subgenus *Anisotarsus*. 127. Ventral aspect of stylus of *mexicana*. 128. Spermatheca and spermathecal gland of *mexicana*. 129. Latero-ventral aspect of valvifer of *cyanippa*. Fig. 130. Latero-ventral aspect of valvifer of female genitalia of *Anisodactylus (Gynandrotarsus) harpaloides*. 131. Sternum VI of female of *Notobia (N.) limbipennis*. 132. Distribution of the subgenus *Anisotarsus*. (Solid dots indicate localities from which one or more species have been collected. Larger open dots represent extensions of species of the *mexicana* lineage into tropical areas or areas surrounded by a tropical climate. The solid dot to the west of North America represents Guadalupe Island while the solid dot to the east represents Bermuda.) (scale lines 1 mm).



Figs. 133-137. Distribution of species of the subgenus *Anisotarsus*. 133. *picea*. 134. *maculicornis*. 135. *nitidipennis*. 136. *lamprota*. 137. *mexicana*.



Figs. 138-143. Distribution of species of the subgenus *Anisotarsus*. 138. *flebilis*. 139. *brevicollis*. 140. *cyanippa*. 141. *schlingeri*. 142. *virescens*. 143. *hilariola*.



Figs. 144-145. Distribution of species of the subgenus *Anisotarsus*. 144. *terminata* (distribution on Bermuda not shown). 145. *purpurascens*.

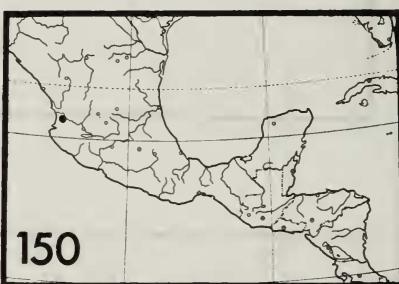
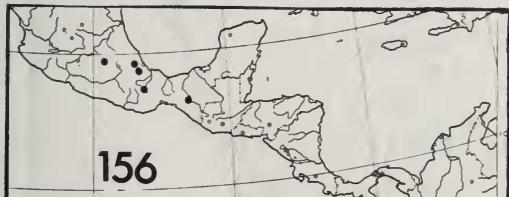
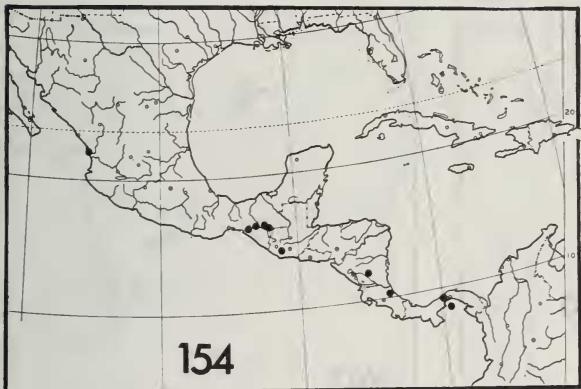
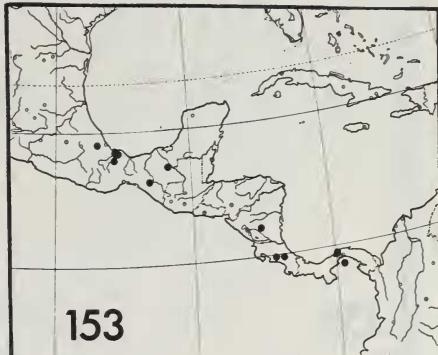
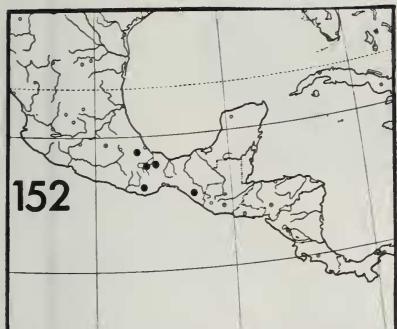
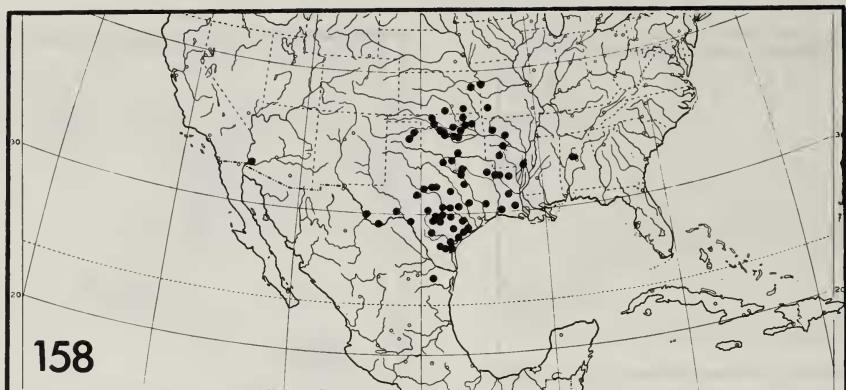


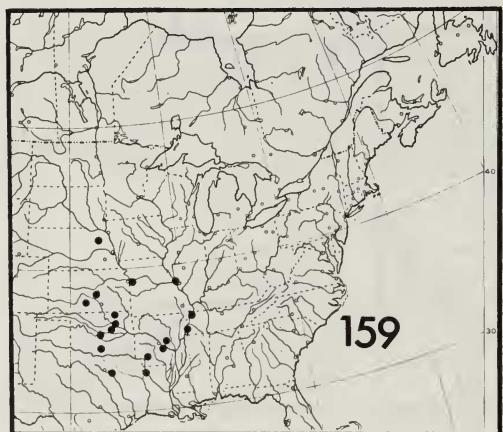
Fig. 146. Distribution of the subgenus *Notiobia*. Figs. 147-151. Distribution of species of the subgenus *Notiobia*. 147. *ewarti*. 148. *umbrifera*. 149. *melaena*. 150. *cooperi*. 151. *leiroides*.



Figs. 152-156. Distribution of species of the subgenus *Notiobia*. 152. *obscura*. 153. *parilis*. 154. *limbipennis*. 155. *umbra*. 156. *pallipes*. Fig. 157. Distribution of *Anisodactylus (Gynandrotarsus) darlingtoni*.



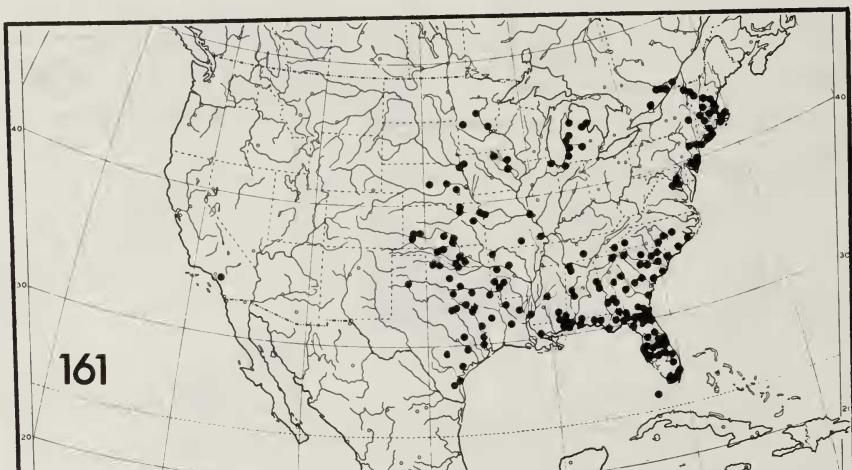
158



159

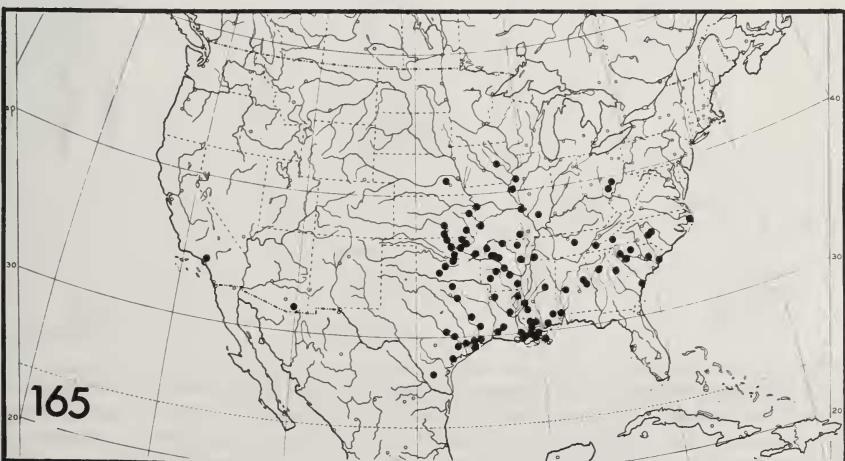
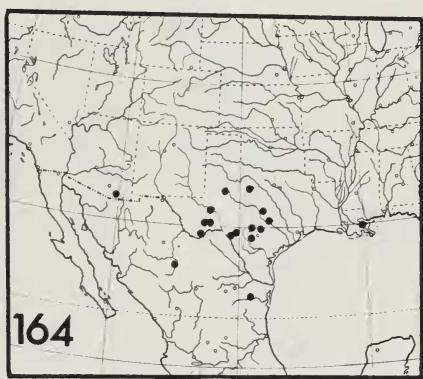
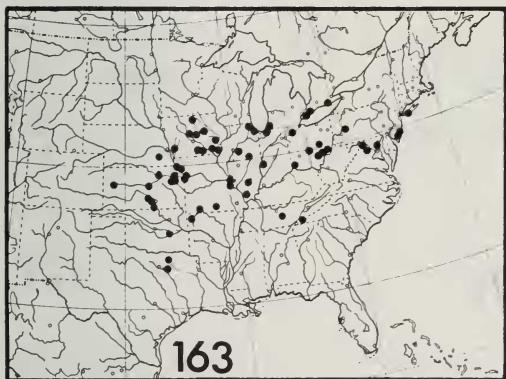
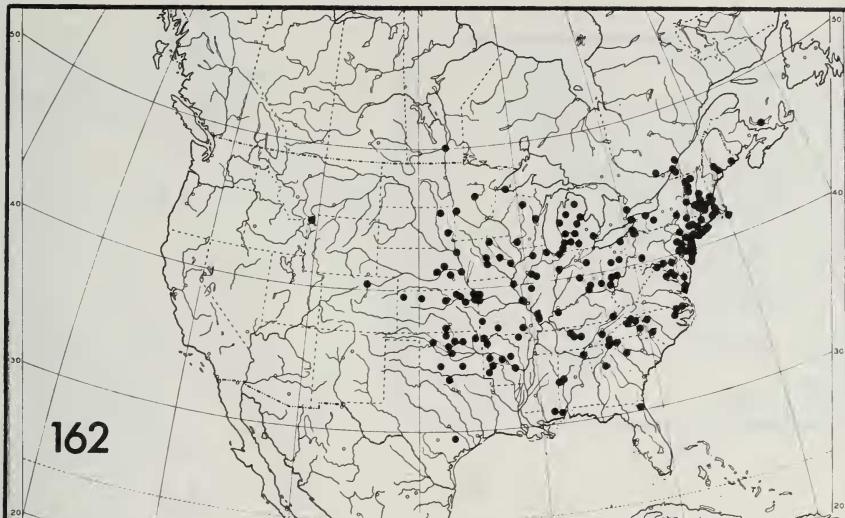


160

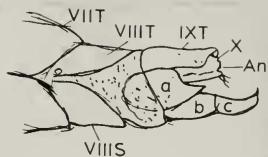
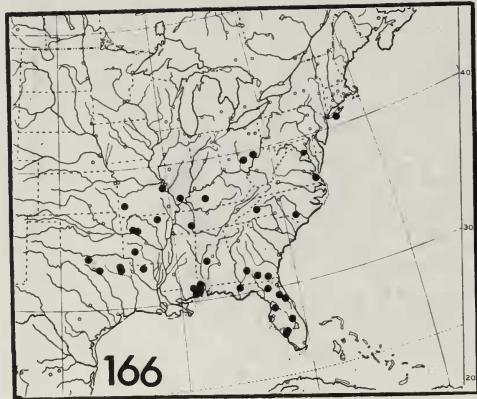


161

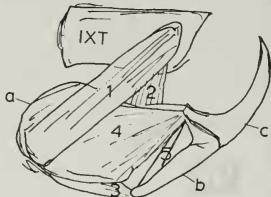
Figs. 158-161. Distribution of species of the subgenus *Gynandrotarsus*. 158. *opaculus*. 159. *harpaloides*. 160. *anthracinus*. 161. *merula*.



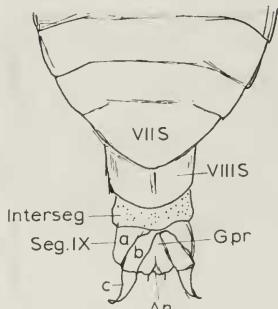
Figs. 162-165. Distribution of species of the subgenus *Gynandrotarsus*. 162. *rusticus*. 163. *ovularis*. 164. *texanus*. 165. *dulcicollis*.



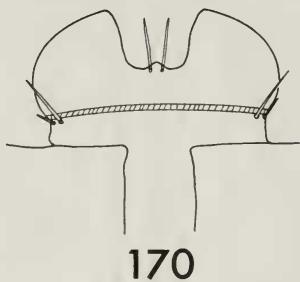
167



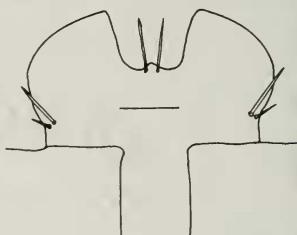
168



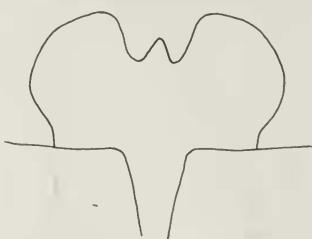
169



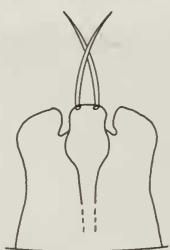
170



171

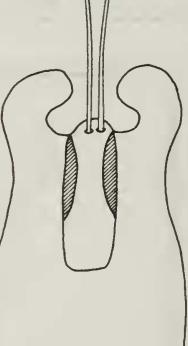


172



173

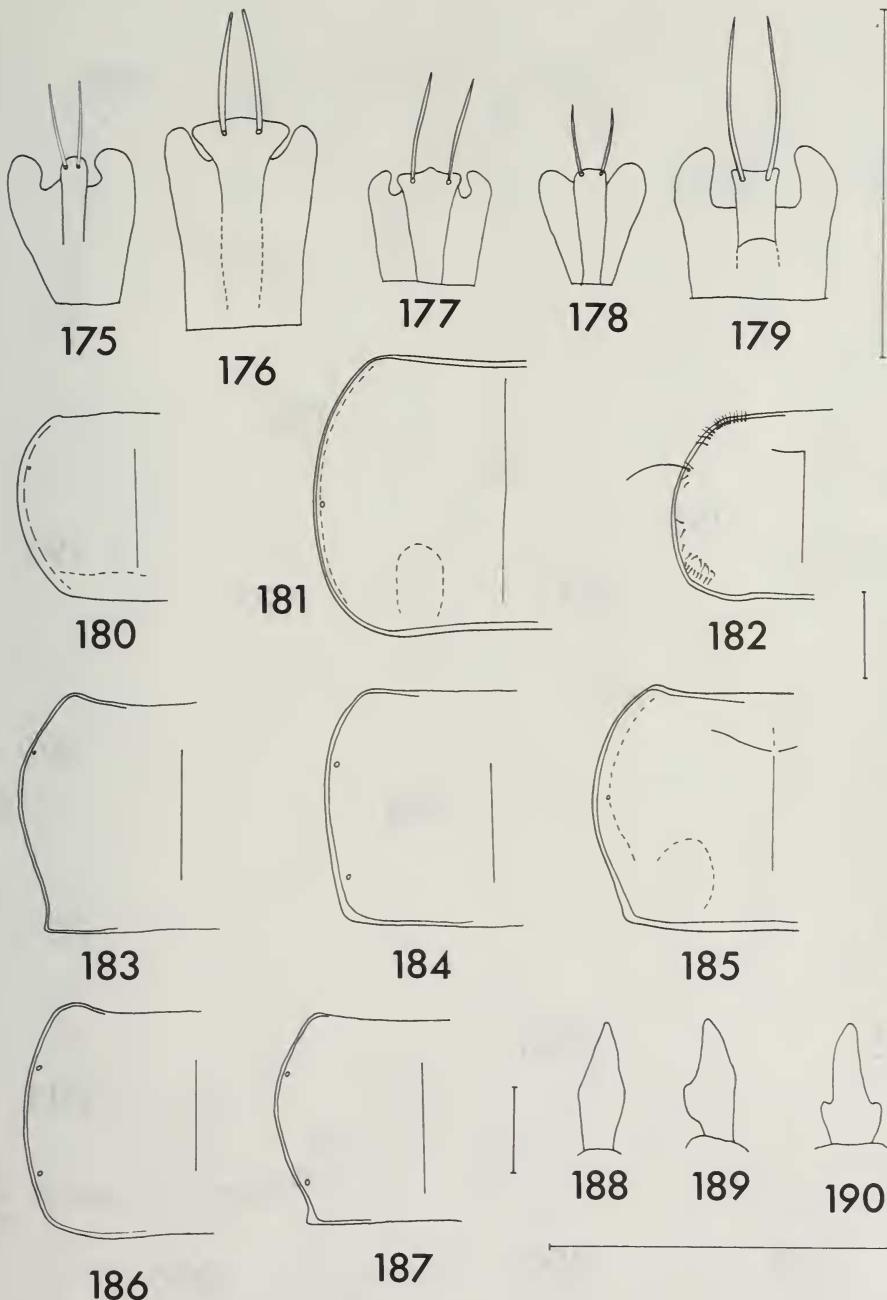
0.5 mm



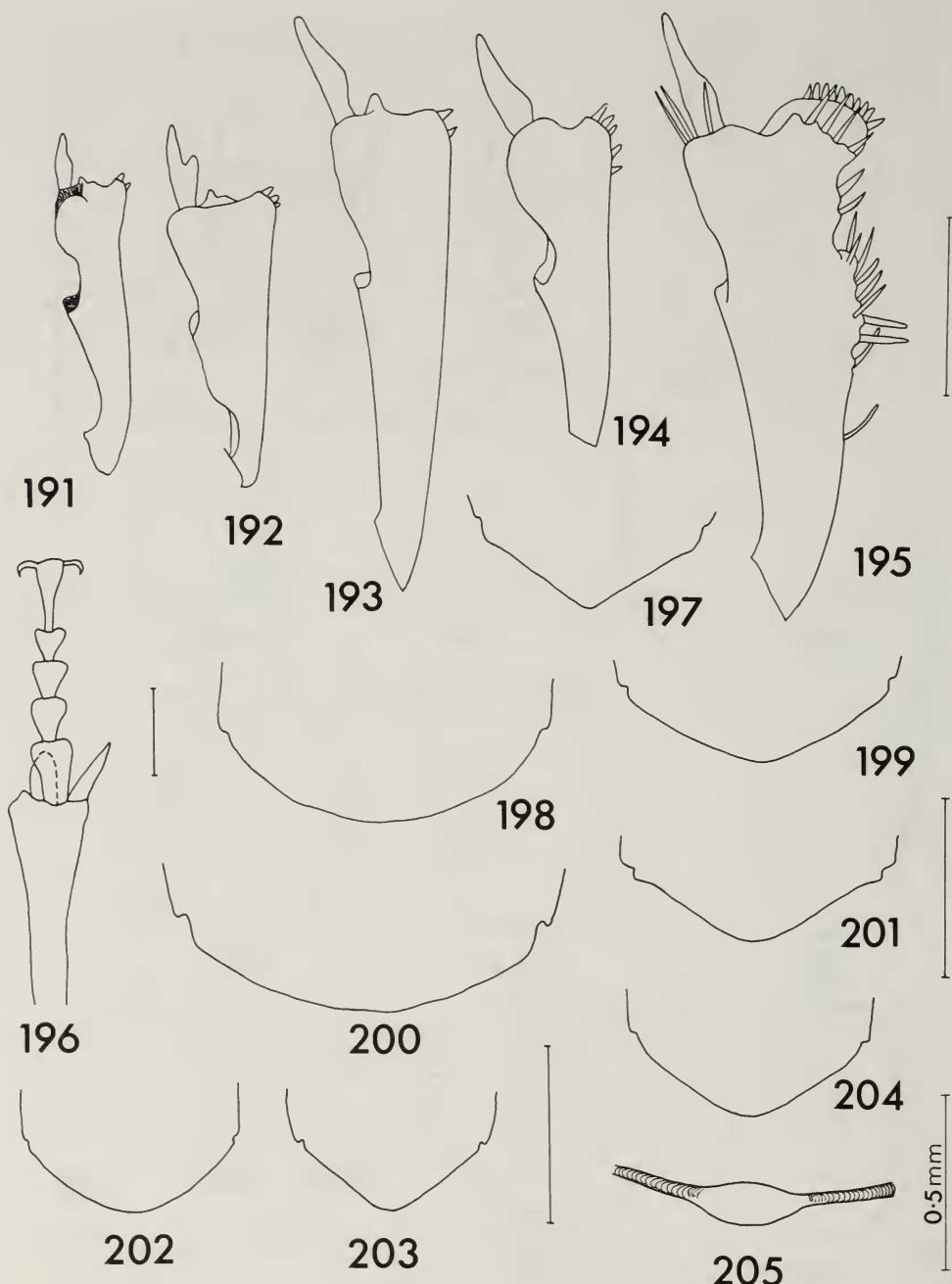
174

0.25 mm

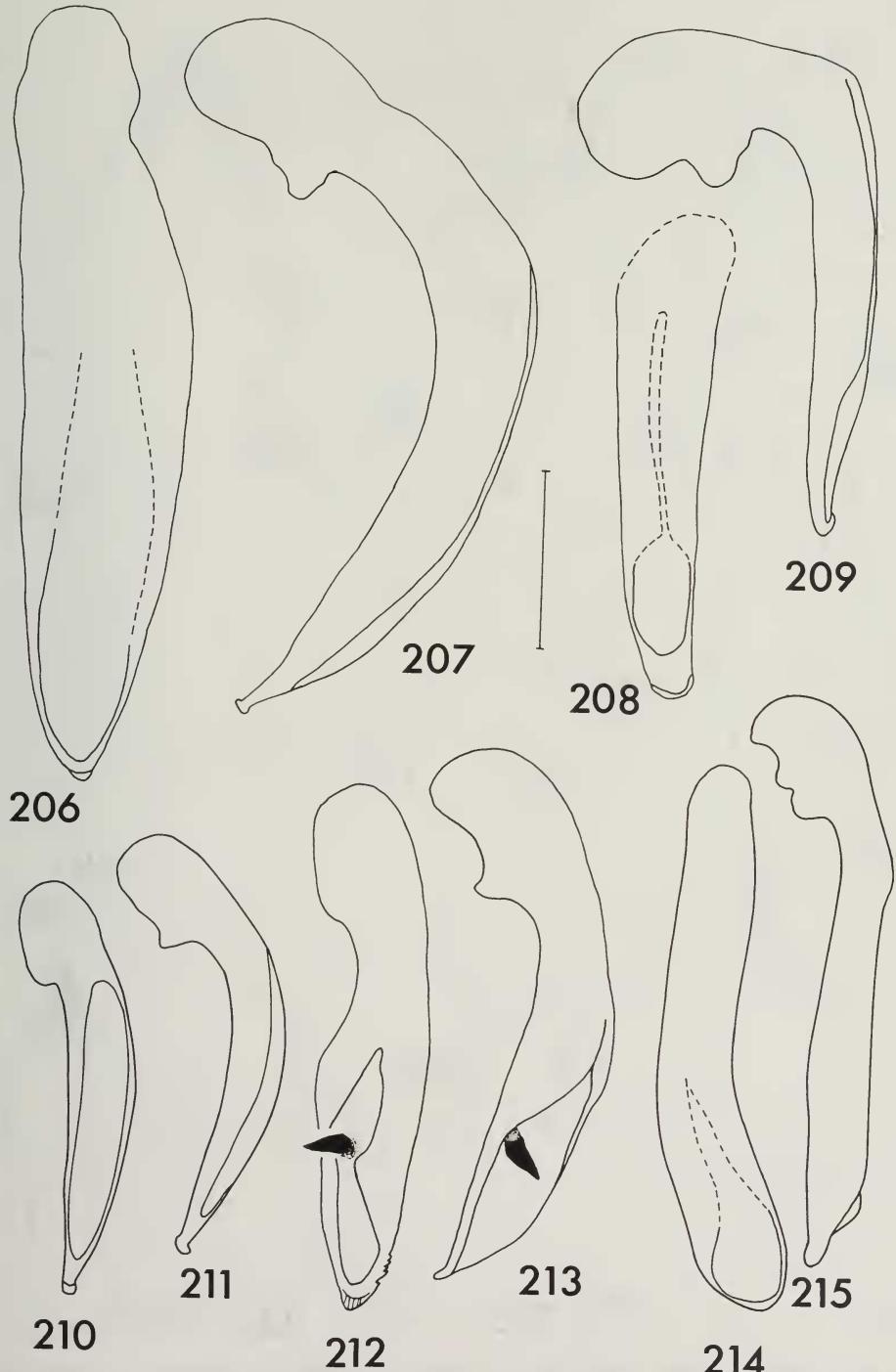
Fig. 166. Distribution of *Anisodactylus (Gynandrotarsus) haplomus*. Figs. 167-169. Unpublished sketches by R. E. Snodgrass of external female genitalia of a species of *Pterostichus*. 167. Lateral aspect. 168. Muscles attached to external genitalia. 169. Dorsal aspect. Figs. 170-172. Mentum and submentum. 170. Notiobiodoid type with suture separating mentum and submentum indicated by hatched area. 171. Anisodactyloid type with mentum and submentum fused and former suture indicated by only a groove. 172. *Chydaeus javanicus*. Figs. 173 & 174. Paraglossa and ligula, ventral aspect. 173. *Xestonotus lugubris*. 174. *Cenogmus castelnau*.



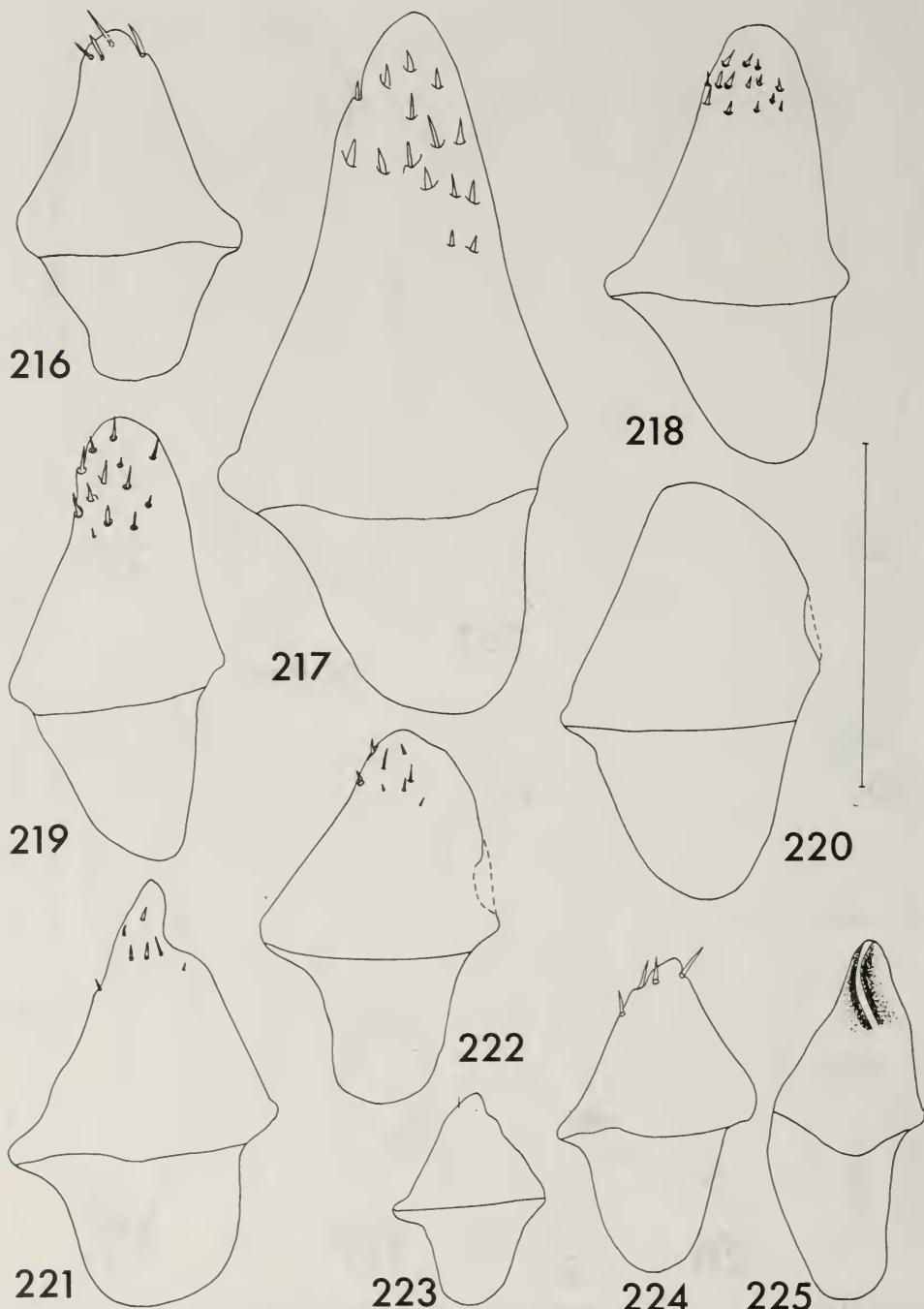
Figs. 175-179. Paraglossa and ligula, ventral aspect. 175. *Anisostichus laevis*. 176. *Anisodactylus (Anadaptus) rotundangulus*. 177. *Amphasia (Pseudamphasia) sericeus*. 178. *Amphasia (A.) interstitialis*. 179. *Anisodactylus (Spongopus) verticalis*. Figs. 180-187. Pronota. 180. *Cenogmus castelnau*. 181. *Crasodactylus indicus*. 182. *Pseudanisotarsus nicki*. 183. *Scybalius hirtus*. 184. *Progonochaetus (P.) caffer*. 185. *Anisodactylus (Spongopus) verticalis*. 186. *Progonochaetus (P.) laevistriatus*. 187. *Progonochaetus (Eudichirus) jeannelli*. Figs. 188-190. Foretibial apical spurs of *Anisodactylus (Anadaptus) nivalis*. 188. Lanceolate shaped form. 189. Form with 1 side angulately swollen (other side may also be so swollen in some specimens). 190. Subtrifid form. (scale lines 1 mm).



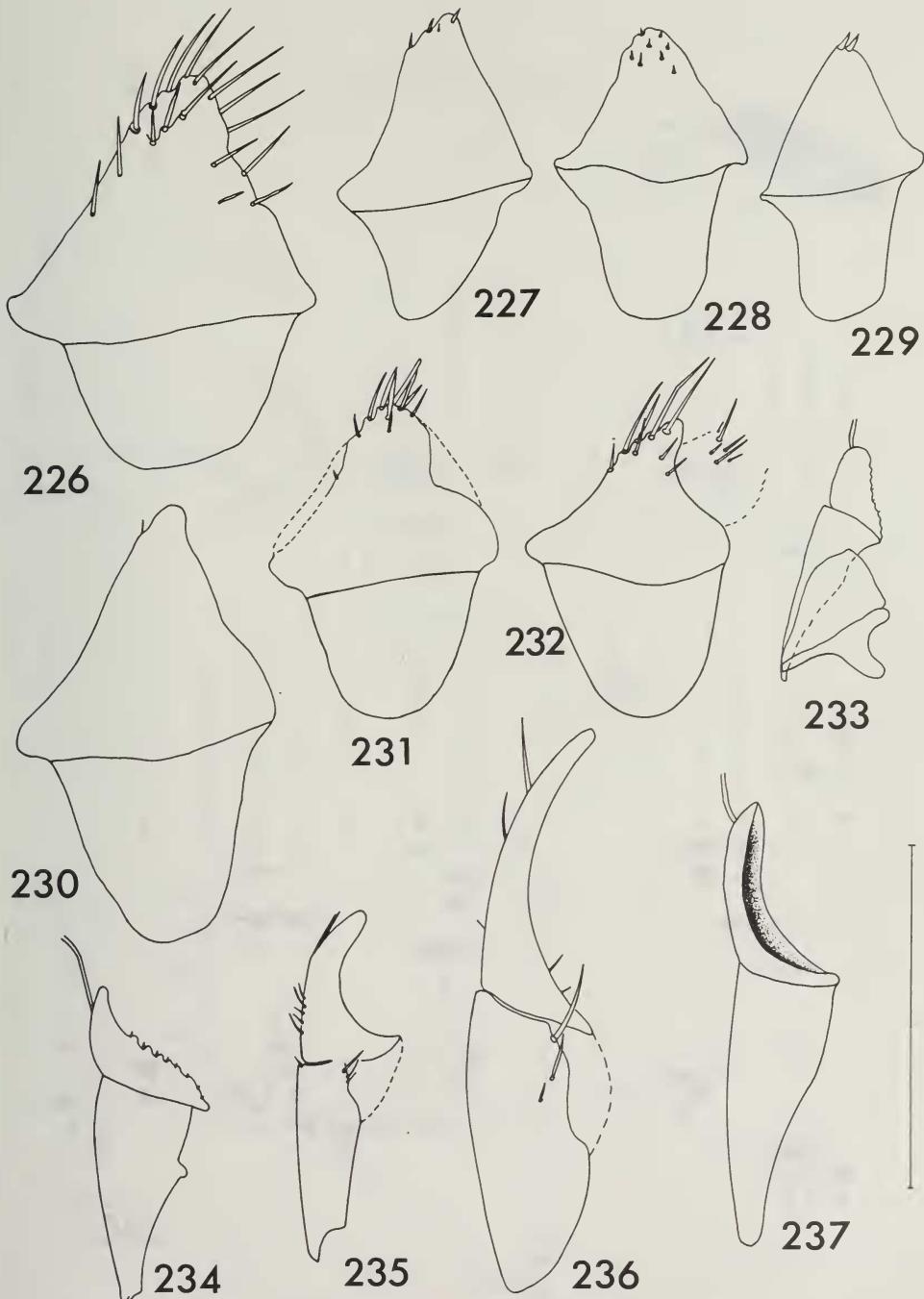
Figs. 191-195. Male foretibiae. 191. *Anisodactylus (Pseudohexatrichus) dejani*. 192. *Anisodactylus (Hexatrichus) poeciloides*. 193. *Anisodactylus (A.) loedigi*. 194. *Anisodactylus (Anadaptus) rotundangulus*. 195. *Geopinus incrassatus*. Fig. 196. Hindtibia and tarsus (setae omitted) *Geopinus incrassatus*, dorsal aspect. Figs. 197-204. Apex of female abdominal tergum VIII. 197. *Gynandromorphus etruscus*. 198. *Anisodactylus (A.) binotatus*. 199. *Anisodactylus (Hexatrichus) poeciloides*. 200. *Geopinus incrassatus*. 201. *Amphasia (A.) interstitialis*. 202. *Anisodactylus (Pseudaplocentrus) laetus*. 203. *Anisodactylus (Aplocentrus) amaroides*. 204. *Diachromus germanus*. Fig. 205. Apex of female *Cenogmus castelnauai* abdominal sternum VI. (scale lines 1 mm unless otherwise labeled).



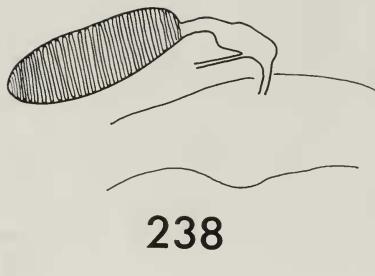
Figs. 206-215. Median lobes of male genitalia. 206 & 207. Dorsal and lateral aspect of *Anisodactylus (Anadactus) rotundangulus*. 208 & 209. Dorsal and lateral aspect of *Scybalicus oblongiusculus*. 210 & 211. Dorsal and lateral aspect of *Notiobia (Diatypus) picinus*. 212 & 213. Dorsal and lateral aspect of *Xestonotus lugubris*. 214 & 215. Dorsal and lateral aspect of *Anisodactylus (Pseudhexatrichus) dejani*. (scale line 1 mm).



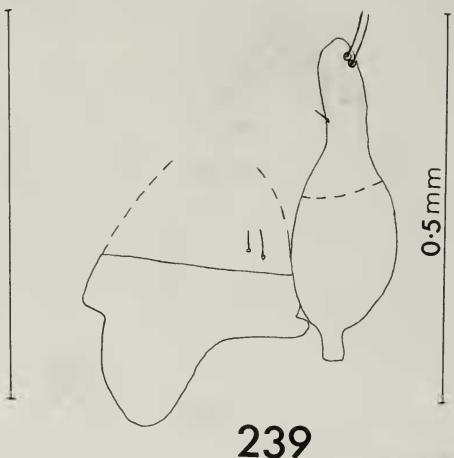
Figs. 216-225. Valvifers of female genitalia, latero-ventral aspect. 216. *Scybalicus oblongiusculus*. 217. *Anisodactylus (A.) loeddingi*. 218. *Anisodactylus (A.) binotatus*. 219. *Anisodactylus (Pseudohexatrichus) dejani*. 220. *Anisodactylus (Pseudodichirius) intermedius*. 221. *Anisodactylus (Pseudanisodactylus) punctatipennis*. 222. *Anisodactylus (Hexatrichus) poeciloides*. 223. *Anisodactylus (Aplocentrus) caenus*. 224. *Anisodactylus (Aplocentrus) amaroides*. 225. *Anisodactylus (Pseudaplocentrus) laetus*. (scale line 1 mm).



Figs. 226-232. Valvifers of female genitalia, latero-ventral aspect. 226. *Geopinus incrassatus*. 227. *Xestonotus lugubris*. 228. *Diachromus germanicus*. 229. *Amphasia (A.) interstitialis*. 230. *Anisodactylus (Spongopus) verticalis*. 231. *Gynandro-morphus etruscus*. 232. *Cenogmus castelnauai*. Fig. 233. Stylus and valvifer of female genitalia of *Amphasia (Pseudamphasia) sericeus*, latero-ventral aspect. Figs. 234-237. Stylia of female genitalia. 234. *Amphasia (A.) interstitialis*, latero-ventral aspect. 235. *Cenogmus castelnauai*, ventral aspect. 236. *Geopinus incrassatus*, latero-ventral aspect. 237. *Anisodactylus (A.) binotatus*, latero-ventral aspect. (scale line 1 mm).



238



239

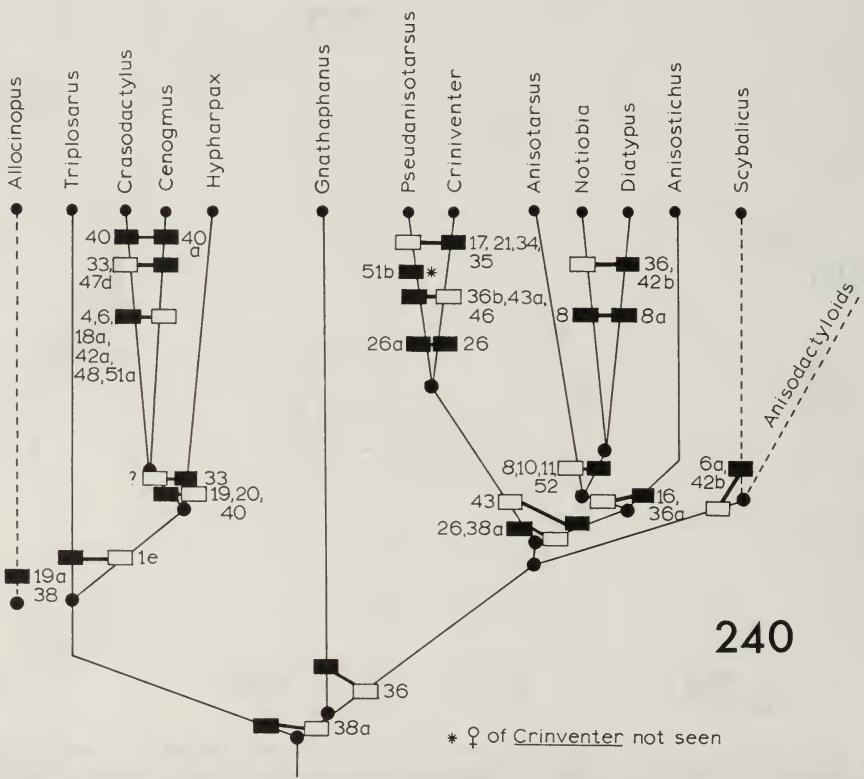


Fig. 238. Spermatheca of female genitalia of *Cenogmus castelnau*. Fig. 239. Valvifer and stylus of female genitalia of *Pseudanisotarsus nicki*, latero-ventral aspect. Fig. 240. Phylogeny of the Notiobioid main branch of the subtribe Anisodactylina. (scale lines 1 mm unless otherwise labeled).

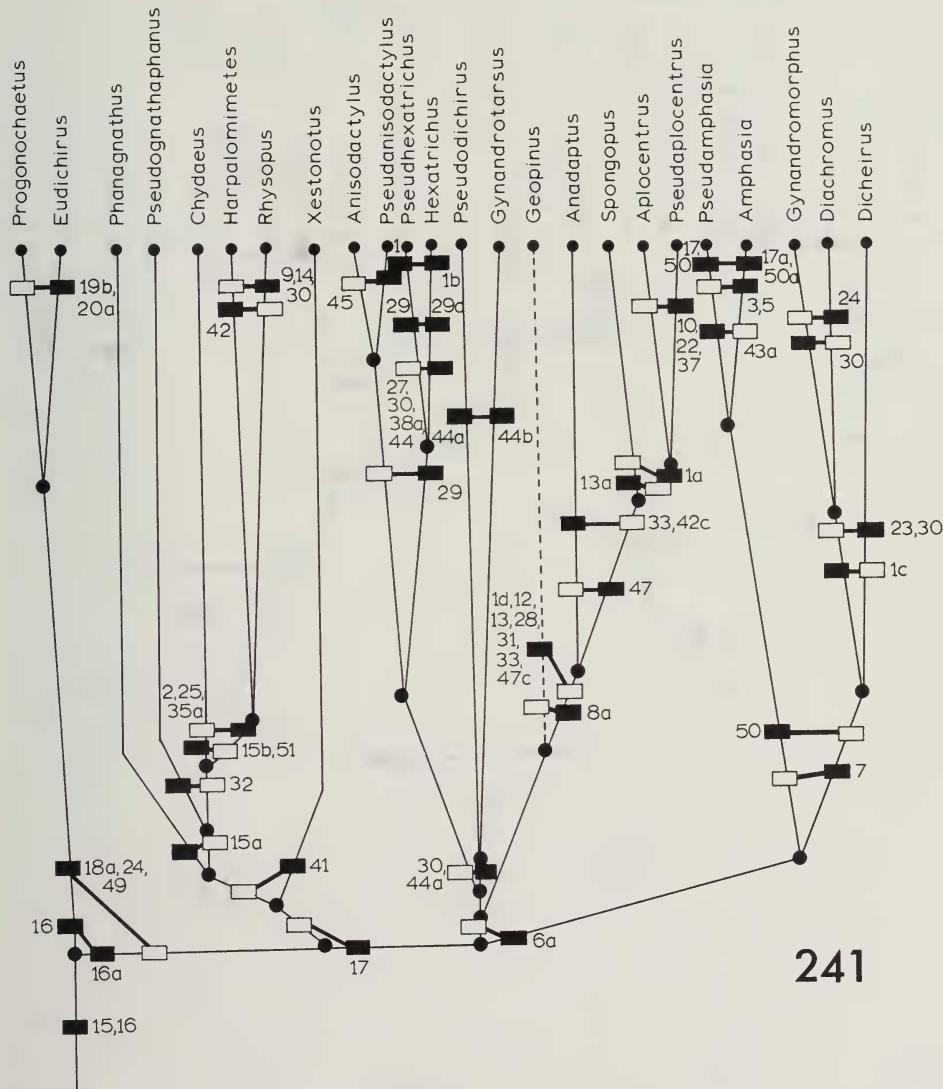


Fig. 241. Phylogeny of the Anisodactyloid main branch of the subtribe Anisodactylina.

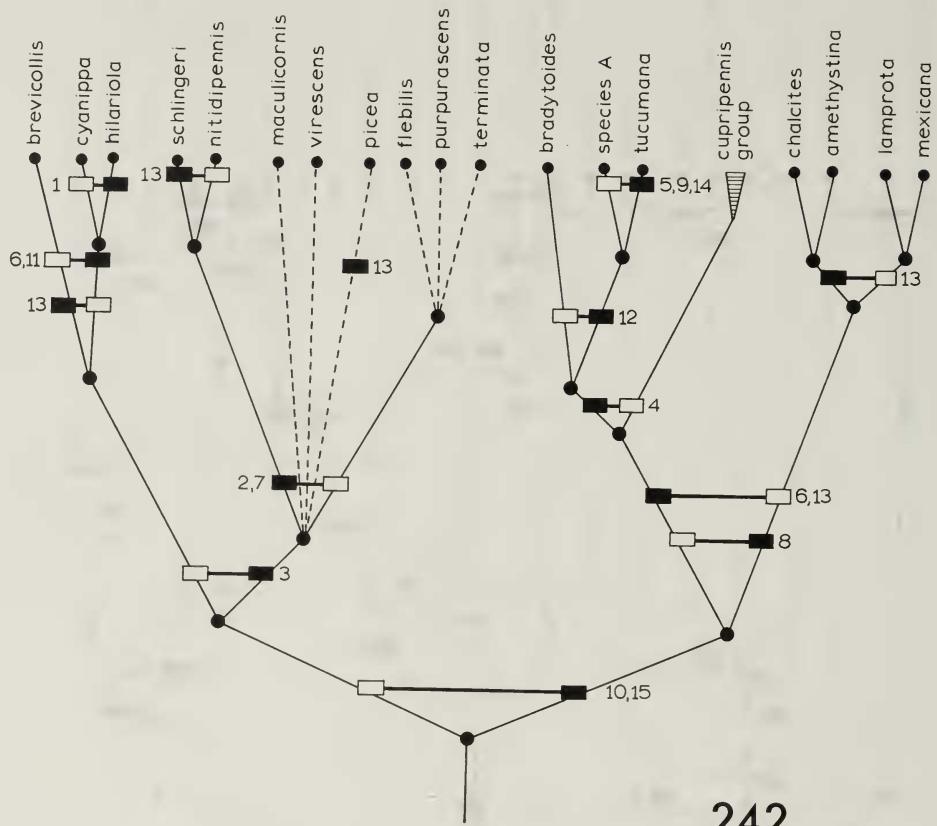


Fig. 242. Phylogeny of the New World species of the subgenus *Anisotarsus* (genus *Notiobia*).

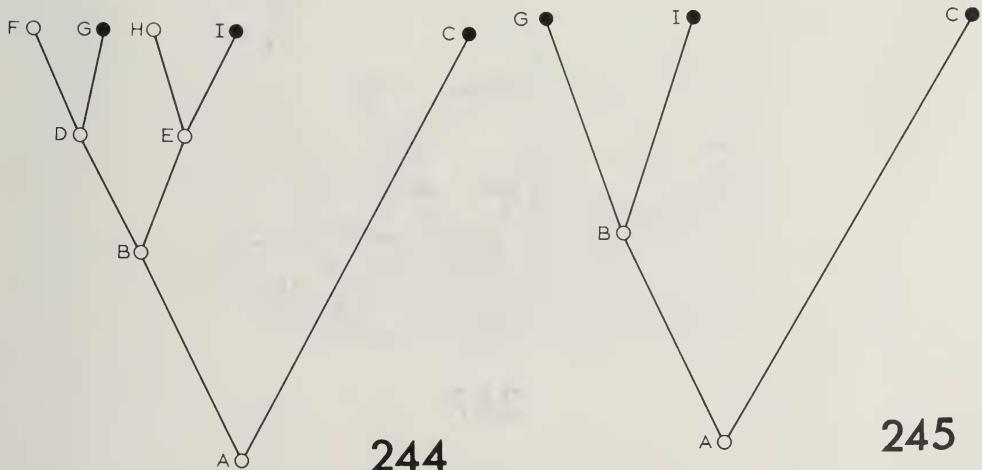
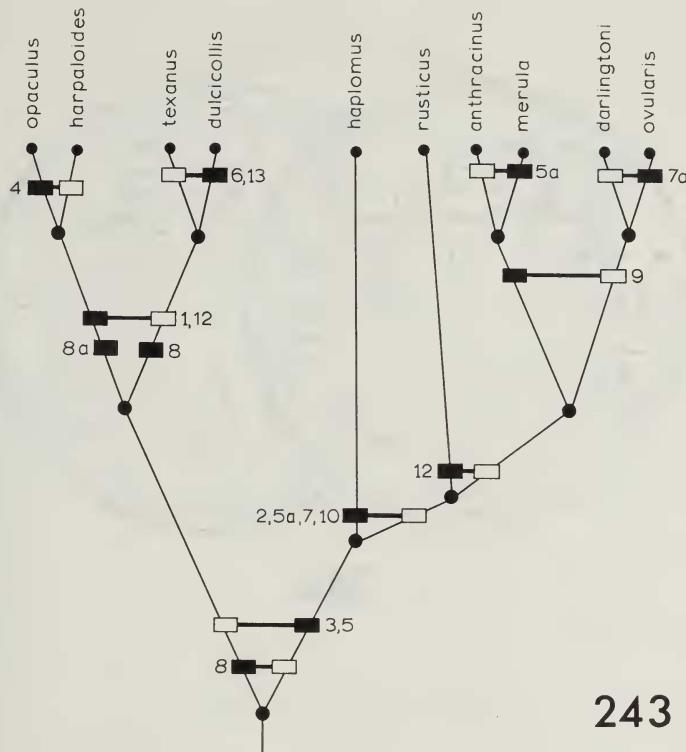
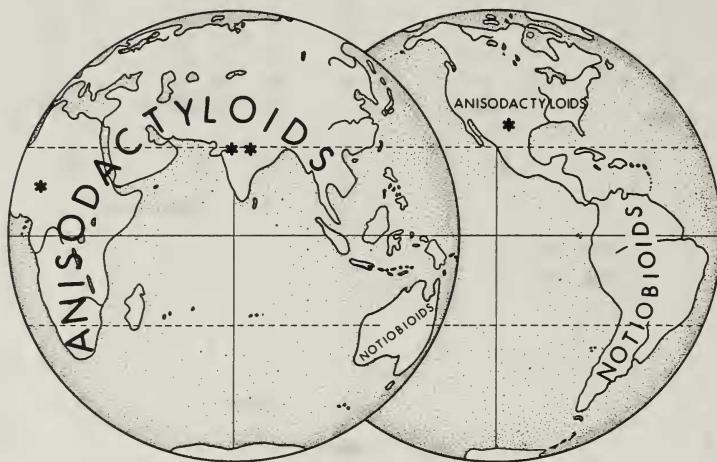
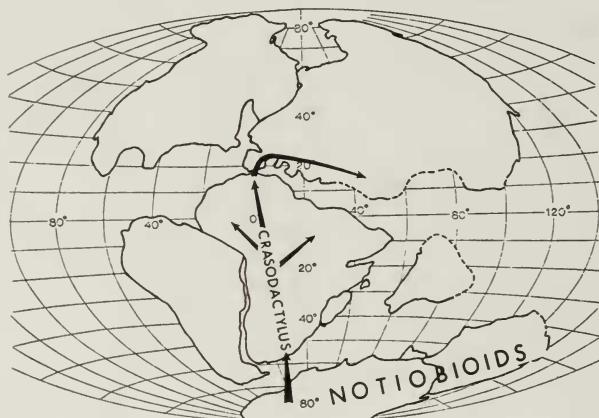


Fig. 243. Phylogeny of the species of the subgenus *Gynandrotarsus* (genus *Anisodactylus*). Figs. 244 & 245. Phylogenies of a hypothetical group of organisms (extinct forms represented by circles, extant forms represented by solid dots). 244. The actual phylogeny of the hypothetical group. 245. The phylogeny of the hypothetical group as reconstructed by a worker dealing only with extant forms.



246



247

Fig. 246. Contemporary distribution of the Notiobioid and Anisodactyloid main branches of the subtribe Anisodactylina (* genus *Notiobia* of the Notiobioids also present in North America and Africa; ** genus *Scybalicus* of the Notiobioids also present in northern Africa and temperate Eurasia). Fig. 247. Postulated crossing in later Jurassic or early Cretaceous of ancestor of *Crasodactylus* to Africa and dispersal to Eurasia (map adapted from Dietz and Holden, 1970).

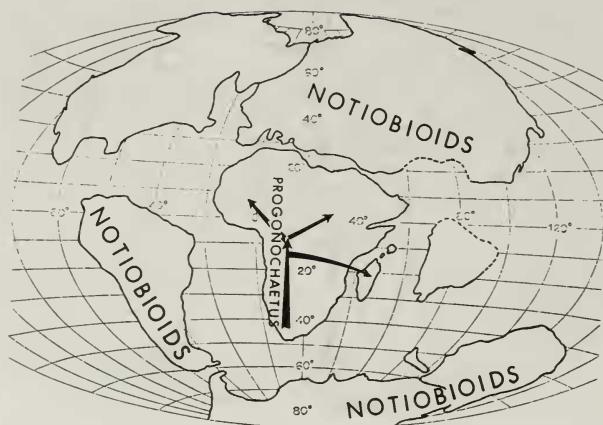


248

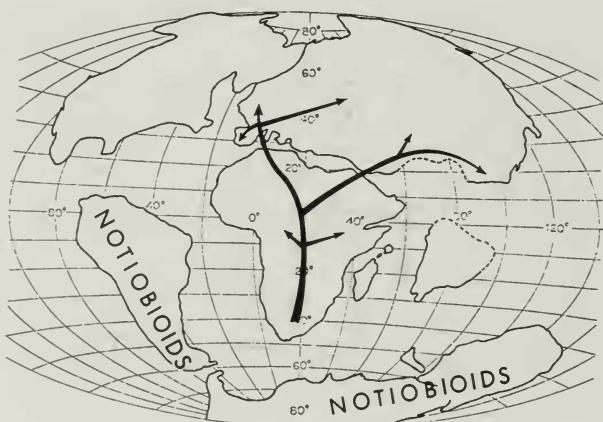


249

Fig. 248. Postulated crossing of member of plesiomorphic *Notiobia* sub-branch in late Jurassic or early Cretaceous to combined continents of South America and Africa and subsequent dispersal northward to combined continents of Eurasia and North America (map adapted from Dietz and Holden, 1970). Fig. 249. Postulated spread of tropical adapted *Notiobia* sublineage throughout tropical portions of northern South America and subsequent crossing into Africa during Cretaceous (map adapted from Dietz and Holden, 1970).

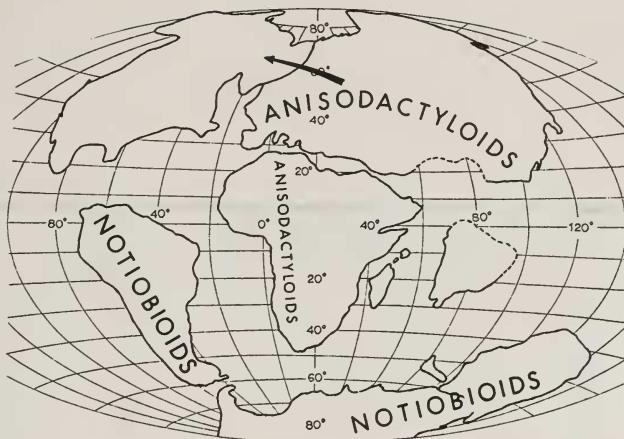


250



251

Fig. 250. Postulated movement northward of first tropical adapted branch of Anisodactyloids to give rise to genus *Progonochaetus* in tropical Africa (map adapted from Dietz and Holden, 1970). Fig. 251. Postulated movement from temperate Africa of second tropical adapted branch of Anisodactyloids and displacement of most Notiobiods from Africa and Eurasia (map adapted from Dietz and Holden, 1970).

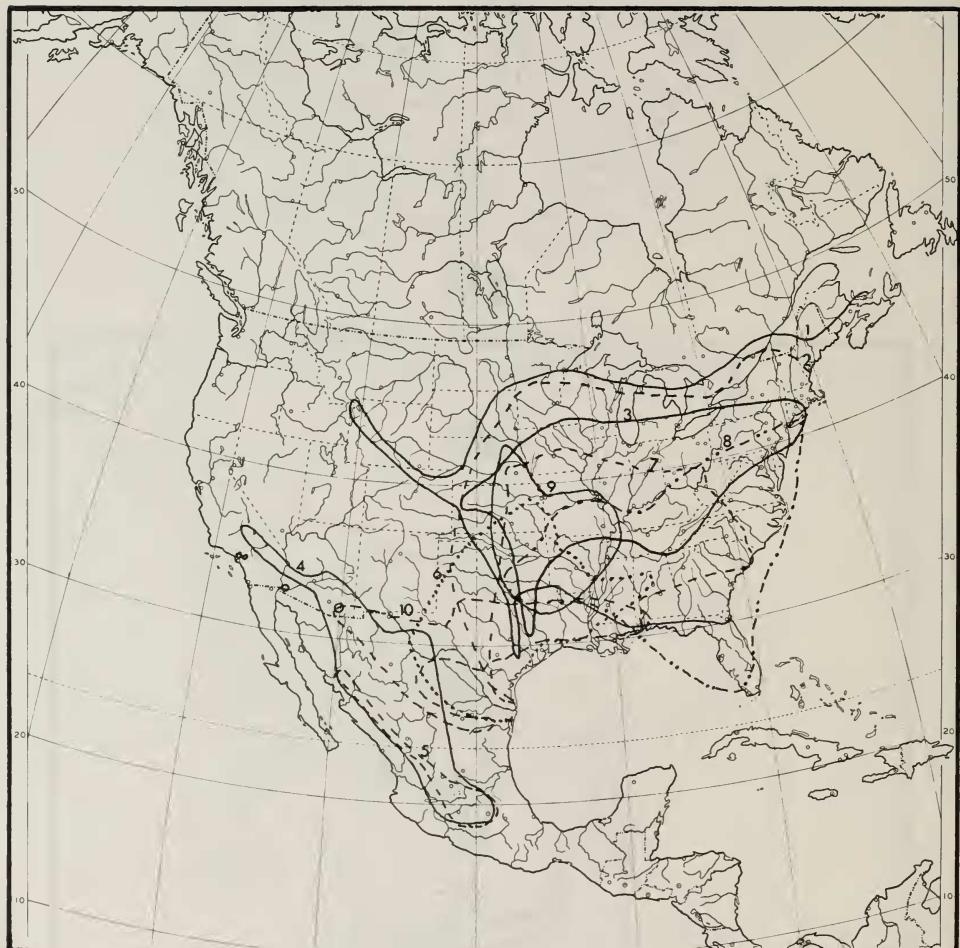


252



253

Fig. 252. Postulated crossing of Anisodactyloids into North America via the land connection with western Eurasia, subsequent extinction of any Notioboids then present in North America (map adapted from Dietz and Holden, 1970). Fig. 253. Outlined ranges of North American species of the subgenus *Anisotarsus* (genus *Notiobia*). Numbers on map refer to species as follows: 1 - *terminata*, 2 - *mexicana*, 3 - *purpurascens*, 4 - *nitidipennis*, 5 - *maculicornis*, 6 - *brevicollis*, 7 - *picea*, 8 - *flebilis*, 9 - *lamprota*, 10 - *hilariola*, 11 - *cyanippa*, 12 - *schlingeri*, 13 - *virescens*.



254

Fig. 254. Outlined ranges of species of the subgenus *Gynandrotarsus* (genus *Anisodactylus*). Numbers on map refer to species as follows: 1 - *rusticus*. 2 - *merula*. 3 - *ovularis*. 4 - *anthracinus*. 5 - *darlingtoni*. 6 - *opaculus*. 7 - *dulcicollis*. 8 - *haplomus*. 9 - *harpaloides*. 10 - *texanus*.